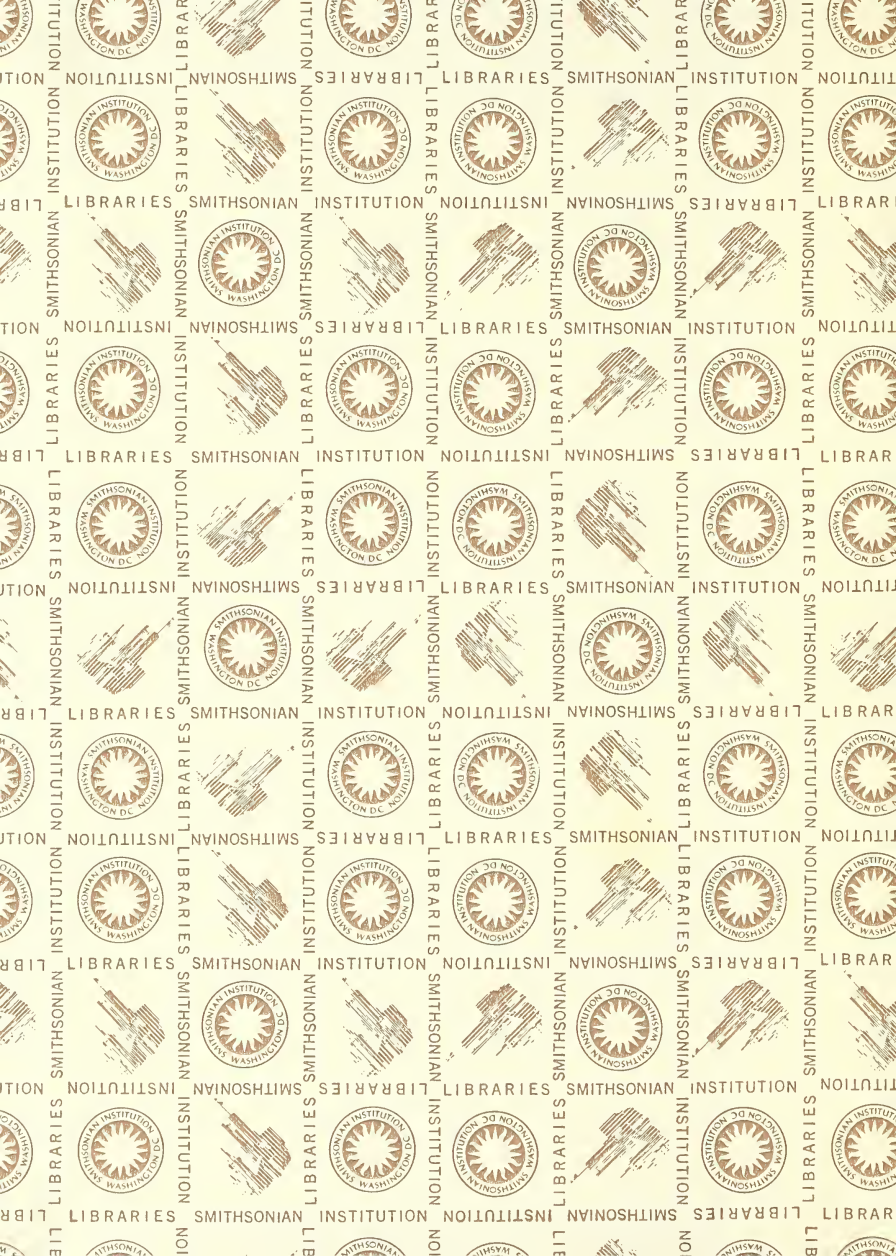
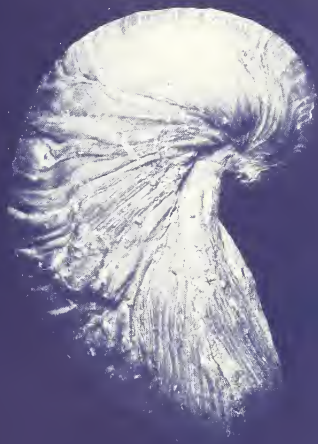
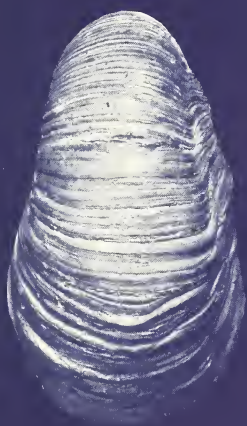






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Cover: The Lower Liassic (Jurassic) oyster *Gryphaea arcuata incurva* J. Sowerby, 1815, from Gloucestershire, England; known popularly as 'The Devil's Toenail'. Specimens in the National Museum of Wales.

TRACES AND TRENDS OF PREDATION, WITH SPECIAL REFERENCE TO BIVALVED ANIMALS

by GEERAT J. VERMEIJ

ABSTRACT. Predation is an ecological interaction which has had a profound impact on the course of organic evolution. Full understanding of this impact can come only when fossil traces of predation are interpreted properly and catalogued systematically. The most reliable traces are those left after unsuccessful attempts by predators to subjugate their prey.

Although predation seems to have increased in evolutionary importance through the course of the Phanerozoic, gastropods and bivalved animals have generally differed in their response to it. Gastropods have tended to emphasize armour, whereas the chief defences of bivalved animals have been escape from and avoidance of predators. The reason for this difference in evolutionary response is hypothesized to lie in the consequences of shell damage. For gastropods, non-lethal damage probably does not increase susceptibility to other causes of death, but for many bivalved animals marginal valve damage increases detectability of the prey because metabolites leach from the soft tissues even when the valves are shut. Accordingly, most pelecypods have very low frequencies of shell repair, and their potential for evolving resistance to breakage is much smaller than that of gastropods.

PREDATION is an ecological interaction which has had a profound impact on the course of organic evolution. Although probable traces of predation date back to the early Cambrian (Pocock 1974), the anecdotal nature of most of the data on these traces has precluded a quantitative understanding of the importance of predation as a component of selection through the course of Phanerozoic time. Moreover, the traces have frequently been misinterpreted, or they have been attributed to non-biological causes. Accordingly, it is appropriate to clarify the meaning of the various traces, to call for more systematic surveys of the traces, and to outline hypotheses about predation over time. These are the aims of this paper.

Predation consists of three more or less distinct phases: the detection or recognition phase, the pursuit or escape phase, and the subjugation or resistance phase (Holling 1966). Predators and prey may show adaptations to each of these phases, but typically adaptation to one phase is better than to the others.

The evolutionary pathways taken by different groups against predators vary. Some groups, like the gastropods, emphasized armour, whereas unshelled cephalopods came to depend chiefly on escape. Pelecypods are conservative and seem to have evolved less conspicuous armour than have gastropods. Their defence lies chiefly in escape or avoidance (Vermeij 1978).

Two important and largely unexplored questions arise from these initial impressions. 1. Does evolutionary emphasis on one form of defence preclude or usurp other types of defence? 2. How are the various pathways of defence determined? I discuss these questions here with special reference to bivalves, whose functional morphology is perhaps better understood than that of any other group of invertebrates. I shall argue that, although adaptation to all phases of predation has increased through time, bivalved animals have had to rely more on escape and avoidance than on armour because of the detrimental consequences of shell damage.

TRACES OF PREDATION

Palaeontologists have available to them three types of evidence of predation. These are: (1) the presence of identifiable remains in faeces (coprolites) or in the stomachs of fossil predators; (2) fossils which have been attacked and killed in a characteristic way by predators; and (3) scars left as the result of unsuccessful attacks by predators. Functional morphology can provide a fourth, less direct, form of evidence. Characters associated in living species with avoidance, escape, or resistance may be interpretable in fossils as antipredatory adaptations if there is some independent evidence that the predator to which the prey had a defence co-occurred with the prey.

Evidence of type 1 provides a direct connection between predator and prey, but it cannot usually yield data on the ecological or evolutionary impact of predation. Although hard parts can be recognized in the coprolites or stomachs of predators, many soft-bodied prey cannot be detected, so that the relative contribution of preserved prey to the overall diet cannot be established. Moreover, the diet of many large, living predatory species is catholic and varies considerably among individuals and from place to place. Accordingly, not too much weight can be placed on the contents of one or a few coprolites or fossil stomachs. Finally, the absence of diagnostic hard parts in preserved faeces or stomachs does not prove that the predator in question did not feed on hard-bodied prey. Crabs, rays, and many other shell-breaking predators ingest only a small fraction of their prey's hard parts, and spit out most of the diagnostic pieces before swallowing the flesh.

Type 2 evidence is difficult to distinguish from postmortem alteration in many cases, but there are exceptions. Drilling predators (gastropods and octopods) leave unambiguous evidence of their activity in the form of holes through the skeleton of their prey. The ecological importance of drilling as a cause of death can be inferred by estimating the proportion of a population of 'dead' shells that has been drilled. The inferred importance of drilling will be overestimated if shell fragments (resulting from lethal breakage) are ignored and if breakage is an important cause of death; it will be underestimated if the prey are sometimes killed without drilling (Vermeij 1980).

The importance of breakage as a cause of death can be inferred if (1) a given break can be recognized as having been lethal; (2) broken and unbroken prey were preserved with equal probability; and (3) breakage was not postmortem (Vermeij 1982a). The first criterion is difficult to satisfy in fossils because it requires that non-lethal damage be distinguished from lethal breakage. Normally, this distinction is possible only after living prey are placed with and damaged by known predators in the laboratory. Differences between prey species may be profound. Destruction of the body whorl, for example, is lethal for short-spined gastropods such as *Conus* and *Strombus*, but is not lethal for such high-spined genera as *Terebra* (Vermeij *et al.* 1980; Vermeij 1982a). The second criterion is likewise difficult to satisfy. Probably the most reliable samples in which to estimate the incidence of lethal breakage are those consisting of uneroded shells in fine sediments where waves or currents are unlikely to have effected large-scale transport. Restriction to samples of this kind also minimizes problems associated with the third criterion. The frequency of postmortem 'lethal' breakage can be estimated in populations in which drilling is a common cause of death. Because drilling gastropods appear to drill chiefly living molluscs and to shun hermit crabs and other secondary shell inhabitants, a drilled 'lethally' broken shell can usually be inferred to have been broken after the mollusc's death. In studies of Recent gastropods (Vermeij 1982a), I have found postmortem breakage to be of relatively minor importance; it inflates estimates of the ecological impact of breakage by no more than 10%. In summary, reliable estimates of the incidence of lethal breakage are unlikely to be obtained for fossil prey species, and difficult to achieve even for Recent species.

The third type of evidence for predation is unsuccessful attack. The incidence of predatory failure provides no information about the ecological importance of predation, but instead permits an evaluation of the role of predation in selection. In principle, selection for antipredatory traits is possible when predators always detect, catch, and subdue their prey. If predators sought out, pursued, and attempted to kill only prey which they could eat, vulnerable individuals would quickly be removed from the prey population and only undesirable or insuperable prey would be left behind to reproduce. Most predators, however, show very high rates of failure during one or more stages of

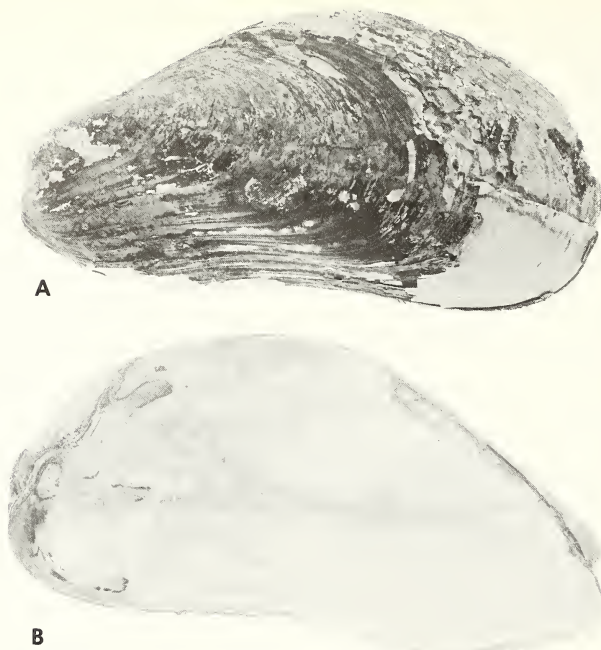
predation (Vermeij 1982b). Although many predators are capable of learning to recognize unsuitable prey and to avoid pursuing or subduing them, learning is accomplished by trial and error, the error being an attempt to acquire unsuitable prey. Moreover, many predators regularly attack unsuitable prey. For all practical purposes, therefore, antipredatory aptation can occur only when predators are frequently unsuccessful in detecting (or encountering), pursuing, or subduing prey (Vermeij 1982b). The prey which evade, escape, or resist predation successfully may differ in subtle ways from prey which are killed. The incidence of unsuccessful attack therefore provides a conservative measure of the potential for antipredatory selection.

It is important to recognize that only certain types and certain phases of predation can be inferred in fossils. Many types of predation leave no diagnostic marks on the prey. When prey are swallowed whole, for example, the predator usually leaves the skeleton intact or disarticulated in unbroken pieces. Even unsuccessful attempts at swallowing may leave no traces. Most predators that attack molluscan tissues by way of the aperture or commissure also leave the skeleton intact, although some damage to the growing edge may occur in some instances. Only predation by skeletal breakage or drilling can leave traces in externally shelled fossils. Unsuccessful predation can be inferred confidently in fossils only for the final (subjugation) stage of predation. Failure to detect or catch the prey may engender strong selection for antipredatory features, but it remains unrecorded in the fossil record.

Repaired skeletal injury is probably the most commonly preserved form of non-lethal predation in fossils. The capacity to repair the skeleton after damage appears to be universal in animals, although the rates of this repair vary widely according to taxon and habitat. Skeletal repair is known in echinoderms (Ebert 1968; Zinsmeister 1980), trilobites (Ludvigsen 1977; Snajdr 1981; Pocock 1974), corals (Loya 1976; Bak *et al.* 1977), brachiopods (Paine 1963; Brunton 1966; Alexander 1981; Jones 1982), and the extant classes of molluscs: Polyplacophora (Tucker and Giese 1959), scaphopods (Papp *et al.* 1947), gastropods (Andrews 1935; Boekschoten 1967; Bulkeley 1968; Currey and Kohn 1976; Geller 1982; and many other references reviewed by Vermeij 1978, 1982b, *in press*), pelecypods (see text-fig. 1) (many reports including Baker 1901; Sykes 1905; Warren 1916; Magalhaes 1948; Yonge 1953; Boshoff 1968; Kauffman 1972; Richardson *et al.* 1980; Savazzi 1981), and cephalopods (Westermann 1971).

The interpretation of shell repair in gastropods is usually straightforward (Vermeij 1982a, b). Most features of armour (thick shell, narrow aperture, capacity to withdraw the soft tissues far into the shell) are associated with a high frequency of non-lethal repaired shell damage. This type of damage results when the outer lip is attacked, broken, and subsequently repaired by the retractable mantle margin of the gastropod. The only type of armour which is not associated with a high frequency of repair is a thickened outer lip. The latter often remains intact even after a vigorous attack. Nevertheless, the frequency of repair serves as a minimal estimate of the importance of shell breakage as a component of selection, and gives an indication of the importance of the shell as an effective fortress.

Shell repair in bivalved animals is somewhat more difficult to interpret than in gastropods. Non-lethal injury of the lip of a gastropod shell does not expose the soft tissues, because the injury does not usually extend beyond the operculum of the retracted animal. Even in species without an operculum, the typical lip injury does not result in exposure of the retracted soft tissues. If it did, the prey would probably be eaten by the attacker. The same applies to injury in scaphopods. For many bivalved animals, however, an injury to the commissure of the valves results in a temporary breach through which metabolites could pass even when the valves are completely adducted. This could be detrimental, because the metabolites released into the environment of an unprotected animal attract potential predators (Christensen 1970; Carriker and Van Zandt 1972; Palmer *et al.* 1982). The capacity to isolate soft tissues temporarily from the outside world is an effective way of avoiding detection by would-be predators which depend on chemoreception. Accordingly, a high frequency of non-lethal marginal injury in bivalved animals indicates not only that the shell and other defences were sufficient to resist subjugation by a predator, but also that the victim was capable of tolerating temporary incomplete closure of the adducted valves. For pelecypods with a permanent anterior or



TEXT-FIG. 1. *Modiolus modiolus* in dorsal (A) and ventral (B) views, showing a remarkable repaired injury. Specimen dredged alive at six to seven fathoms depth off St. Andrews, New Brunswick, Canada, September 1982.

posterior gape, such as many temperate deep-burrowing mactrids, myacids, and solenids (Vermeij and Veil 1978), marginal damage might not be very detrimental because it does not substantially increase the prey's detectability, but for species which can normally seal off the soft tissues completely a marginal injury could increase susceptibility to other causes of death.

There seem to be at least two fundamental ways in which bivalved animals can prevent marginal damage from breaking the seal between the adducted valves. First, the edges of one or both of the valves may extend beyond the line of contact between the valves. The commissure lies in a furrow between the slightly projecting valve edges in some venerid and fimbriid pelecypods, and is tucked in beneath the projecting edge of either the right or left valve in the Corbulidae and some Arcidae. This latter protection of the commissure is associated with an inequivalve condition (Nicol 1958; McGhee 1978; Lewy and Samtleben 1979). It is extremely rare in brachiopods; only some Permian richthofeniids, oldhaminids, and lyttoniaceans had the brachial valve recessed within the pedicle valve (Rudwick 1961; Rudwick and Cowen 1967; Williams and Hurst 1977). Another variation on the theme of commissural protection is the development of spines or scales which project well beyond the line of contact between the valves, as in spondylid and some chamid pelecypods and in some

upper Palaeozoic strophomenide brachiopods (Stanley 1970; Rudwick 1970). The second mechanism preventing marginal damage from being lethal is mantle retraction. A highly retractable mantle edge coupled with a thin, flexible prismatic distal portion of the valves is characteristic of pinnacean and pteriacean pelecypods (Yonge 1953; Carter 1980). When the valve edges are bitten or chipped, the mantle can be withdrawn and the break temporarily sealed between the remaining flexible surfaces of the opposing valves. Valve flexibility does not seem to have evolved in articulate brachiopods (Carter 1980), but some strophomenides had the anterior edges of their valves extended with very little space between the adducted valves (Rudwick 1970). The hypothesis that these methods of commissural protection indeed permit non-lethal marginal damage and the eventual evolution of breakage-resistant armour has not been tested.

Some pelecypods and brachiopods may have overcome the problem of marginal damage by evolving globose shells in which the seam between the closed valves blends in with the smooth contour of the shell as a whole. When a potentially shell-breaking predator attacks, the edge is no more vulnerable than are other parts of the shell. If the attack is unsuccessful, the shell remains undamaged. Smoothly contoured globose shells are present among some arcid, corbulid, and shallow-burrowing lucinid pelecypods and among many rhynchonellide brachiopods. Again, the suggested protective function of globosity in preventing marginal damage requires experimental confirmation.

If the soft tissues were toxic or repellent to an intruder, a marginal break would not necessarily increase risk of death to the victim, even if more animals were able to detect the metabolites diffusing from the animal. I know of no documented examples of intrinsic toxicity in pelecypods, although temporary toxicity due to infestation by dinoflagellates is widespread. C. W. Thayer has unpublished data suggesting that articulate brachiopods from Puget Sound may be repellent to predaceous crabs, fishes, asteroids, and gastropods. The apparent rarity of toxicity in pelecypods is surprising, but it is consistent with the edibility of most pelecypods to humans.

Because non-lethal shell damage may increase the detectability of bivalves to potential predators, the geographical and temporal patterns in the incidence of shell repair in bivalved animals may be quite different from those in gastropods. Both the development of breakage-resistant shell armour and the frequency of non-lethal shell injury in gastropods increase from the temperate zones to the tropics, from fresh to salt waters, from the tropical Atlantic to the tropical Pacific and Indian Oceans, and through time from the Palaeozoic to the late Mesozoic and Cenozoic (Vermeij 1978, 1982b; Vermeij *et al.* 1980; Vermeij and Currey 1980; Palmer 1979; Bertness *et al.* 1981). In pelecypods, the incidence of permanently gaping species, which typically burrow deeply into unconsolidated sediments, declines from high to low latitudes (Vermeij and Veil 1978), while the incidence of tight closure (as reflected in the incidence of crenulate valve margins) increases toward the tropics (Vermeij 1978). These patterns suggest the following hypotheses: (1) predation by animals which penetrate between the valves becomes evolutionarily more important toward the tropics; and (2) detection by predators is more strongly selected against at low latitudes than at higher latitudes. Moreover, temperate bivalves may be able to sustain greater injury than their warmer-water counterparts. Accordingly, the incidence of non-lethal marginal breaches may be greater at higher latitudes than in the tropics. Marginal damage which does not expose the soft tissues when the valves are shut should be more common in the tropics, as is lip damage in gastropods.

A preliminary analysis of my unpublished data on mussels (Mytilidae) shows frequencies of repair in this family to be extremely low and not to change with latitude. Yet mussels are frequently attacked by crabs, birds, and other potential shell-breakers which often fail to kill their prey (Ebling *et al.* 1964; Harger 1972; Elnor 1978; Griffiths and Seiderer 1980).

Other work in progress suggests that the incidence of marginal repair in fresh-water unionid pelecypods is very high. Nearly every shell of some thick-shelled species from the central and southern United States bears scars. In some respects, this might be expected if chemoreceptive predators are rare in fresh waters, but the observation of high frequencies of marginal repair in fresh-water clams leads to a curious paradox. Unionids may often be exposed to stronger selection in favour of breakage-resistant armour than are marine pelecypods, in which the threat of chemical

detection may be very much greater. This situation contrasts strongly with that in gastropods, where armour and repair are both much more common in marine species. If these patterns are borne out, they point to the possibility that selection for one form of defence often depends on the importance of other selective factors.

PREDATION THROUGH TIME

It has been suggested that armour in gastropods increased in incidence and in degree of expression through the course of the Phanerozoic (Papp *et al.* 1947; Vermeij 1975, 1977). During the middle and late Palaeozoic, gastropods with mechanically weak features (umbilici, loose coiling) comprised more than 25% to 30% of the species in most local assemblages, whereas forms with breakage-resistant features (narrow aperture, thick outer lip, strong tuberculate sculpture) were rare or absent. Beginning in the middle Jurassic, a shift took place in gastropod architecture, so that gastropods with breakage-resistant traits and with the capacity to withdraw the body far into the shell expanded in numbers at the expense of mechanically weak forms. By the late Cenozoic, species with apertural modifications comprised more than 20% of most tropical assemblages, whereas umbilicate forms were found in fewer than 10% of species (Vermeij, in press). The hypothesis that breakage became an increasingly important component of selection after the Triassic is supported by data showing that the frequency of predator-induced shell repair increased after that time (Vermeij *et al.* 1981). P. Signor suggests that early Palaeozoic gastropods were even less well armoured than were their middle and late Palaeozoic descendants, and that the Devonian was a time of architectural change as important as the Jurassic. Armour also increased in ammonoids, in which the frequency of strong sculpture and of complexly fluted sutures increased gradually, if not constantly, from the Devonian to the late Cretaceous (Ward 1981).

It may be possible to make a similar case for increasing armour through time in bivalved animals, but critical experiments linking specific shell features to breakage-resistance have not been done, and temporal patterns in these features have not been documented in detail. At the microstructural level, several groups of pelecypods have evolved shells of foliated calcite, which permits the development of strengthening radial plications, as in Mesozoic and Cenozoic Pectinidae (Waller 1972). Oysters (mostly post-Permian Ostreacea) and several sedentary Pectinacea and Cretaceous Hippuritacea have evolved calcitic shells in which cavities may limit the spreading of incipient cracks (Carter 1980). On the other hand, it has been shown that nacre is typically stronger (with respect to compression) than are other types of molluscan microstructure (Currey and Taylor 1974; Currey 1976, 1977), yet nacre is also the primitive microstructure in pelecypods and gastropods (Taylor 1973; Carter 1980). The evolutionary abandonment of nacre in favour of prismatic, foliated, crossed-lamellar, and other microstructures in many lineages argues strongly against an increase in shell strength over time at the microstructural level. Palmer (in press) has now shown that gastropods with nacreous structure, in which the organic content is higher than in other microstructural types, regenerate shell more slowly than do gastropods with crossed-lamellar structure.

Radial and concentric sculptures thicken and perhaps sometimes buttress the shell of pelecypods and brachiopods. In infaunal forms, these types of ornament also promote anchorage or burrowing in the sediment. Among infaunal pelecypods, external ornament was rare during the Palaeozoic (e.g. *Astartella*), but it became widespread with the rise to dominance in the Triassic and Jurassic of the Trigoniacea and the hegemony of the heterodonts in the Cenozoic (Stanley 1977a, b, 1981). Thick shells are another obvious defence against shell-breakers, but I have no data on changes in the occurrence of thick-shelled bivalved taxa over time.

Stanley (1970) remarked with justifiable surprise that epifaunal pelecypods are often thinner-shelled than their shallowly burrowing infaunal relatives. This is evident, for example, in the Carditacea and Arcacea of the modern world ocean. The only epifaunal taxa that have distinctly thick shells are cemented forms (Ostreacea, Chamacea), large byssally attached giant clams (Tridacnidae), and some small Arcacea and Carditacea living under stones; but many shallow-burrowing infaunal taxa have shells that are as thick as or thicker than those of species from beneath

boulders. These observations highlight the paradox that, although attached epifaunal pelecypods would be readily available targets for attack by shell-breakers, many of these animals have not adopted exceptional armour as their chief defence.

I believe that the explanation for this paradox lies in the poor capacity of bivalved animals to sustain even slight marginal damage. In order to evolve armour, animals must survive episodes of damage-inducing attack (Vermeij 1982b). In bivalved animals, however, marginal damage often invites predators or other potential agents of death to a damaged individual. Accordingly, it may be difficult in general for bivalved animals to sustain and survive shell damage. As pointed out above, exceptions may occur among taxa with highly retractable mantle margins and flexible valve margins, and among species in which the valves project beyond the commissure. Armour would be expected to evolve only among taxa with these attributes, at least as a defence against shell breakage.

Initial support for this hypothesis comes from data on the incidence of repaired marginal breaks in Recent pelecypods. In temperate and tropical mytilids, donacids, and venerids I have examined, the frequency of repair is typically extremely low, almost never rising above 0.15 scars per shell. Many samples show no repair. The only species I have encountered so far with plentiful repaired damage is the shallow-burrowing venerid *Anomalocardia flexuosa* from Brazil, in which I have found frequencies of up to 0.70 scars per individual. In their survey of six common pelecypods from the Pliocene of Albenga, Italy, Robba and Ostinelli (1975) found repair in only two species, *Anadara diluvii* (0.07) and *Corbula gibba* (0.35). The latter species is characterized by a thick shell of which the right valve ventrally overlaps the smaller left valve.

The underlying assumption that marginal damage is detrimental to bivalved animals still requires confirmation. I know of no data in the literature bearing on this point.

Those who are sceptical of the above arguments will counter that many epifaunal pelecypods are, after all, thick-shelled and therefore well armoured. Examples include many cemented forms, giant clams, and a few very large mytilids. In this connection it is important to remember that thickened valves are advantageous for many reasons. One advantage is protection against muricacean drilling gastropods, whose attempts to drill are frequently unsuccessful (see Vermeij 1982b, for a review). Unsuccessful drilling can lead to strong selection for thick shells. Although drilling predation is known throughout most of the Palaeozoic and Mesozoic eras, it did not become quantitatively important until the late Cretaceous (Vermeij 1977; Sohl 1969; Vermeij and Dudley 1982). It may therefore prove difficult to separate drilling from breakage as a cause for the evolution of thick-shelled pelecypods.

If many pelecypod groups did not emphasize armour as a defence, they did respond to increasing selection from predators by escaping or avoiding their enemies. Stanley (1970, 1975, 1977a, b, 1981), who has studied shell features which promote burrowing, notes that these features were rare during the Palaeozoic, but became widespread during the Mesozoic and Cenozoic. Sculpture of the ratchet type, in which the anterior and ventral flanks of ribs are less steep than the posterior and dorsal flanks, aids some venerids, cardiids, trigoniids, and tellinids in burrowing and in gripping the sediment (Stanley 1977b, 1981). Ribs of this morphology appeared for the first time in Mesozoic Trigoniacea, and are common today in tropical, shallow-burrowing pelecypods and infaunal gastropods (see also Signor 1982). Pelecypods with smooth, glossy, streamlined shells, which are associated with rapid burrowing, are known only in Cretaceous to Recent families such as the Veneridae, Donacidae, Tellinidae, and Mesodesmatidae (Stanley 1977a). Runnegar (1974) points out that deep-burrowing late Palaeozoic anomalodesmatans had the umbones placed anterior to the shell's midline, whereas many deep-burrowing post-Palaeozoic members of this group have the umbones in a more posterior position. He interprets this change as reflecting an increase in the size of the foot and a change from a ventral to an anterior position of the pedal gape. These changes in relative foot size and orientation may mean that post-Palaeozoic Anomalodesmata from deep sediments are better burrowers than were their late Palaeozoic counterparts (Runnegar 1974). Modern cockles (Cardiidae) are typically faster burrowers than *Neotrigonia*, a relict living representative of the functionally equivalent but chiefly Mesozoic family Trigoniidae (Stanley 1977b). Sedentary epifaunal pelecypods and brachio-pods on unconsolidated bottoms were very common in the Palaeozoic, but these types of animals

waned after the Permian except in deep waters, where inoceramids remained important until the late Cretaceous. Animals of this type are essentially absent from the Recent fauna. The only pelecypods that live on the surface of unconsolidated sediments are very large (the tridacnid *Hippopus*), byssally attached, or mobile (Pectinacea, *Placuna*) (Stanley 1977a; Thayer, in press). These trends suggest that mobility, especially burrowing, became increasingly important to the survival of pelecypods through time. I interpret this increased emphasis on mobility to be a response to an increase in the importance of predation as a component of selection in pelecypods.

Thayer (in press) interprets the rise of mobile suspension-feeders at the expense of sedentary reclining forms as a reflection of the increasing importance of sediment disturbance (bioturbation) over the course of the Phanerozoic. Certainly this possibility cannot be discounted; indeed, it is likely that both predators and bioturbation were responsible for the increased emphasis on mobility in pelecypods. It may be that increased bioturbation is itself a manifestation of an increase of predation at and above the sediment surface.

Another theme which runs through the evolutionary history of pelecypods is that of predator avoidance. Stanley (1972, 1977a) noted that semi-infaunal byssally attached pelecypods were widespread during the Palaeozoic, but today survive chiefly in sediments which are stabilized by the roots of marine angiosperms. Predators in such vegetated sediments are much less effective at finding prey than they are in unvegetated sands (Peterson 1979, 1982; Heck and Thoman 1981). The increased emphasis on tight closure and the largely post-Palaeozoic occupation of deep sediments by pelecypods may be other expressions of the increasing emphasis on predator avoidance by pelecypods. With respect to the latter trend, Blundon and Kennedy (1982) have shown that deeply burrowing clams stand a greater chance of remaining undetected by burrowing crabs than do clams which are buried more shallowly.

Another possible evolutionary response of bivalved and other animals to predation is a reproductive one. Some species may have no morphological or behavioural defences against predators, but instead may have fecundities that are so high that the prey population is maintained even in the face of intense predation on adults. Whether this response can legitimately be classified as an antipredatory aptation in the sense of Vermeij (1982b) is a matter of personal opinion, but in any case little can be said about its incidence in the modern fauna or about its evolutionary history.

Although analysis of groups other than gastropods and bivalved animals is beyond the scope of this paper, increasing emphasis on armour or escape through the course of the Phanerozoic seems to characterize most groups of animals. I interpret these patterns to mean that predation in general has become increasingly important in determining the morphology and distribution of marine invertebrates. Groups which, for one reason or another, have been unable to evolve effective armour or methods of escape survive today only in physiologically marginal habitats where predators are slow or rare (Vermeij 1978). I believe that the gradual occupation of such environments, including deep sediments and the cold deep sea, was one consequence of the increasing evolutionary impact of predation through the Phanerozoic.

Predation is by no means the only, or even the primary, cause for the observed architectural and ecological changes through time. Competition for scarce resources probably also intensified over the course of the Phanerozoic, and indeed may be fundamental to the evolution of enhanced predatory capabilities in many groups (Vermeij, 1982b). The importance of predation is often easier to assess than that of interactions such as competition, parasitism, or mutualism, but this does not mean that these other relationships were less important.

One of the unique contributions that palaeontologists can make to the study of evolution is the documentation of trends or of the lack of trends through time. This documentation will require large-scale surveys of the occurrence of architectural traits in groups from different periods, the incidence of traces of predation, and the importance of other biological relationships between organisms. These surveys should encompass all species in the community, not just those in which a given phenomenon is particularly common. Studies of interactions between a few chosen species from one formation in one period are interesting and often important, but in the context of the documentation of long-term trends they are anecdotal and therefore potentially misleading. Further-

more, it is important to compare spatial variation with temporal variation. Inevitably, there is much variation in the incidence of unsuccessful predation and in almost every other aspect of biological interaction from place to place, even when the habitats are much the same (Vermeij *et al.* 1981). Without an awareness of such variation, it is difficult to evaluate the reality of purported temporal trends.

Many questions remain to be answered. How did the major episodes of mass extinction influence the observed trends? Were the trends temporarily reversed, or was the pattern of selective extinction such that the trend toward greater antipredatory aptation was accentuated? Was the increase in gastropod armour during the mid-Mesozoic stimulated or accelerated by the breakup and dispersal of the continents? More generally, is the increase in defence to be expected from first principles of evolution, as suggested by Darwin (1872), or were the trends driven by extrinsic historical factors of geography, climate, and crisis? These questions will challenge palaeontologists for years to come.

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MICROBIOTAS OF THE LATE PRECAMBRIAN RYSSÖ FORMATION, NORDAUSTLANDET, SVALBARD

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ABSTRACT. Silicified carbonates of the uppermost Riphean (800–700 Ma) Ryssö Formation, Nordaustlandet, Svalbard, contain abundant, well-preserved microfossils that represent several palaeoenvironmental settings, life habits, and trophic modes. The fossils fall into three distinct assemblages. A stromatolitic microflorule preserved in flat cryptalgal laminated cherts includes seven taxa: three mat building cyanobacteria, two mat-dwelling or probable mat-dwelling blue-greens, one allochthonous element, and one rare species of indeterminate ecological role. An open coastal planktonic assemblage contains fourteen distinguishable taxa, including many acritarch species that have commonly been found in Upper Riphean shales and siltstones. The third assemblage is dominated by organically preserved skeletons and siliceous casts of vase-shaped heterotrophic protists. Collectively, these assemblages provide an unusually broad picture of microbial life in the Late Proterozoic Era. The Ryssö Formation contains twenty-one taxa, of which one, *Scissilisphaera regularis* gen. et sp. nov., is formally described as new.

It is well known that the record of Precambrian microbial life observable in thin sections of silicified carbonates differs significantly from that found in macerations of ancient siliciclastic rocks. The differences are real and, in large part, ecological in origin, reflecting the predominantly benthic nature and restricted environmental setting of most 'cherty' microbiotas and, in contrast, the planktonic nature and normal marine setting of the large organic-walled microfossils that are common in late Precambrian shales.

The distinctive taxonomic and palaeoecological differences between cherty carbonate and siliciclastic biofacies present an interesting problem for palaeobiological reconstruction of late Proterozoic life. This problem is compounded by occurrences in uppermost Riphean and lower Vendian rocks, both siliciclastic and carbonate, of dense populations of vase-shaped microfossils interpreted as the remains of heterotrophic protists. Where these distinctive fossils are well preserved, other fossils are often poorly fossilized or absent.

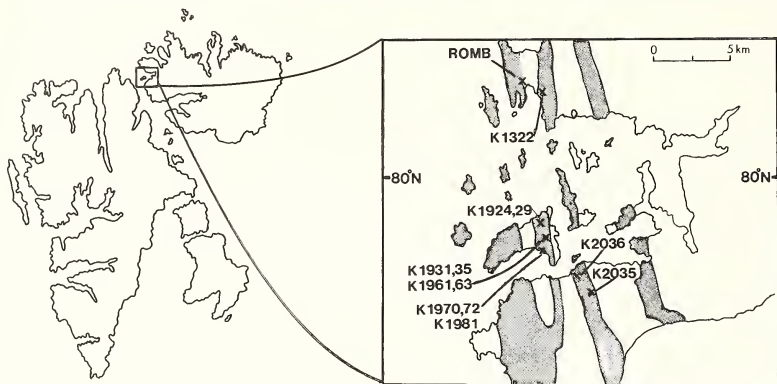
All three types of microfossil assemblage are necessary to provide the breadth of evidence required for critical interpretations of late Proterozoic biology. Rarely does a single formation contain all three assemblage types, but one unit that does is the uppermost Riphean (800–700 Ma) Ryssö Formation exposed in Nordaustlandet, Svalbard. In providing a record of both benthic and planktonic life, open coastal to intertidal habitats, and both primary producers and heterotrophs, the Ryssö biota contributes to the construction of an integrated picture of late Precambrian life.

GEOLOGICAL SETTING AND AGE

In the Murchisonfjorden region of western Nordaustlandet and in adjacent north-eastern Spitsbergen, approximately 6000 m of folded but essentially unmetamorphosed Upper Proterozoic sedimentary rocks lie atop an older series of metavolcanics and metasediments (Odell 1927; Harland *et al.* 1966; Harland and Wright 1979). The unmetamorphosed sedimentary deposits of western Nordaustlandet have been placed in the Murchisonfjorden Supergroup and divided into four groups: the Gotia Group (600 m), an uppermost detrital series containing conspicuous tillites; the Roaldtoppen Group (1300 m), a thick series of dolomites and limestones with associated cherts and shales; the Celsiusberget Group (2100 m), composed predominantly of shallow water

sandstones and siltstones; and the lowermost Franklinsundet Group (1800 m), a succession of limestones, quartzites, and shales (Flood *et al.* 1969; Harland and Wright 1979).

The Ryssø Formation is located stratigraphically within the Roaldtoppen Group. It conformably overlies the fossiliferous, predominantly dark limestone Hunnberg Formation (see Knoll 1983) and is in turn overlain by carbonaceous mudstones of the lower Gotia Group. No unconformity is visible at the Ryssø/Gotia contact, but palynological investigations suggest that a significant time gap separates the depositions of the two units (Knoll 1982b). The Ryssø Formation is the dominant geological feature of the Murchisonfjorden area (Kulling 1934;



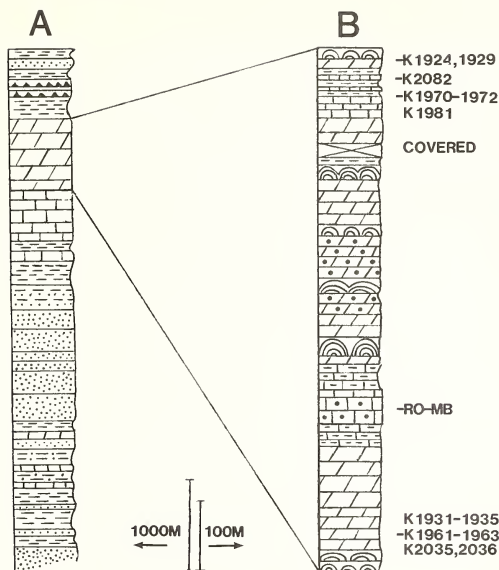
TEXT-FIG. 1. Location map showing the position of the Murchisonfjorden area (boxed and enlarged region) within Svalbard. Outcrop area of the Ryssø Formation is indicated by stippling. Fossiliferous localities are noted on the map.

text-fig. 1). Text-fig. 2 shows a stratigraphic section of the Ryssø Formation measured by Flood *et al.* (1969) on Söre Russøya, a large island in the middle of Murchisonfjorden. Except for minor intercalations of shale and quartzitic sandstone, the formation consists throughout of dolomite and dark bituminous limestones. Columnar and domal stromatolites are common throughout the formation, as are flat laminated cryptalgal beds. Oolites and pisolites occur in the lower half of the formation along with intraformational edgewise conglomerates, shallow channels, and occasional low angle cross-beds. It is apparent that the entire formation was deposited in coastal carbonate flat environments ranging from intertidal to very shallow subtidal marine.

Silicification is common in microbially laminated dolomites near the base of the formation, as well as in associated carbonate conglomerates. Chert also occurs as replacements of oolites and pisolites, in thin originally carbonate beds within a predominantly black shale unit near the top of the formation, and, rarely, as nodules and lenses in 'algal' dolomites near the top of the section. In all cases, the silica appears to be of early diagenetic origin. Many of the cherts are carbonaceous and it is in these rocks that most Ryssø microfossils are preserved, although scattered specimens have also been obtained by maceration of black shales.

Existing radiometric dates place few constraints on the timing of Ryssø deposition, but two independent lines of biostratigraphic evidence provide a reliable age estimate for the formation. Columnar stromatolites collected by A. A. Krasil'shchikov in 1963 and 1964 have been extensively studied by Soviet palaeontologists. Identified forms include *Gymnosolen murchisonicus* Golovanov, *Inseria blingica* Gol., *I. clunbergica* Gol., *Jacutophyton spitsbergensis* Gol., *Yungulsia* sp., *Kussiella* (?) sp., and *Conophyton* sp. (Milstein and Golovanov 1979). Raaben and Zabrodin (1969) also report the presence of *Boxonia granulosa* and *Tungussia russa* in the Ryssø Formation. On the basis of columnar stromatolites, a Late Riphean (approximately 950 to 700 Ma) age is suggested for the formation (Golovanov and Raaben 1967; Raaben and Zabrodin 1969; Milstein and Golovanov 1979).

Soviet workers have also employed microphytolites (oncolites) as biostratigraphic indicators. A Late



TEXT-FIG. 2. Generalized stratigraphic columns for the Upper Proterozoic Murchisonfjorden Supergroup in Nordaustlandet (A) and the Ryssö Formation (B). Black circles within carbonate symbols indicate oolites and pisolites. The stratigraphic positions of fossiliferous localities are indicated in column B. Stratigraphy modified from Flood *et al.* (1969).

Riphean to Vendian age for Ryssö deposition is suggested by Milstein and Golovanov (1979) on the basis of microphytolite distribution.

The reliability of columnar stromatolites in stratigraphic correlation has been widely debated (see Walter 1977, for a fair appraisal of both sides of the argument), and the use of microphytolites as biostratigraphic markers has enjoyed little support outside the Soviet Union; however, an independent and reliable scheme for the subdivision and correlation of late Precambrian sequences is provided by the organic walled remains of eukaryotic plankters which radiated in Late Riphean and early Vendian times (Timofeev 1959, 1969; Vidal 1976, 1981a, b; Vidal and Knoll 1983). Robust-walled planktonic microfossils, usually referred to as acritarchs (e.g. Downie 1973), are widespread geographically and lithologically in Upper Proterozoic sequences, have limited and delimitable stratigraphic ranges, and are easily identified. Thus, they constitute excellent fossils for biostratigraphic correlation on an international scale.

Table 1 lists the acritarchs recognized in the open coastal planktonic assemblage of the Ryssö Formation. This is a typical Late Riphean assemblage, comparable to previously described microbiotas from Europe and the Soviet Union. A Late Riphean depositional age is supported by the stratigraphic first appearance of vase-shaped microfossils in the upper third of the formation. These distinctive fossils have been found on four continents, and where their biostratigraphic context is well known, they appear near the top of the Riphean sequence and continue into lower Vendian beds (Knoll and Vidal 1980). Their presence in the Ryssö Formation may indicate that this formation accumulated late in the Late Riphean interval. In round figures, one can broadly estimate the age of the formation as 800 to 700 Ma.

TABLE 1. Microfossils present in the Ryssö Formation. Fossils are listed by assemblage along with their size (diameters or, for filaments, cross-sectional diameter) and inferred paleoecological role. For species occurring in more than one assemblage, size data are presented only once.

	Size range (and mean diameter) in μm	Paleoecological interpretation
I. Stromatolitic assemblage		
<i>Siphonophycus kestron</i> Schopf	9–18 (14.3)	Common mat builder
<i>Eomycetopsis robusta</i> Schopf emend. Knoll and Golubic	2–4 (2.6)	Common mat builder
<i>Tenuofilum septatum</i> Schopf	0.5–1.5 (1.0)	Rare mat builder
Multilamellated sheath	39	?
<i>Myxococcoides</i> spp.	9–30	Allochthonous (planktonic?)
<i>Coniunctophycus</i> sp.	2–9 $\times$ 2–6 (3.1 $\times$ 2.3)	Locally common mat dweller
<i>Scissilisphaera regularis</i> gen. et sp. nov.	11–45 (18.2)	Locally abundant mat dweller (?)
II. Coastal Plankton Assemblage		
<i>Chuarina circularis</i> Walcott	180–800 (282)	Common plankton
<i>Kildinella hyperborea</i> Timofeev	22–70 (43)	Common plankton
<i>Kildinella sinica</i> Timofeev	23–76 (40)	Common plankton
<i>Trachysphaeridium laufeldi</i> Vidal	72	Rare plankton
<i>Trachysphaeridium levis</i> (Lopukhin) Vidal	56–92 (74)	Rare plankton
<i>Trachysphaeridium</i> sp. A of Knoll (1983)	42–65 (54)	Common plankton
<i>Trachysphaeridium</i> sp. B of Knoll (1983)	220–450 (268)	Rare plankton
<i>Trachysphaeridium vidalii</i> Knoll	210–255 (241)	Rare plankton
<i>Phanerosphaerops capitans</i> Schopf	43–57 (49)	Rare plankton
<i>Pterospermopsis</i> sp.	150–172 (161)	Rare plankton
cf. <i>Stictosphaeridium</i> sp. (<i>sensu</i> Vidal, 1976)	43–130 (78)	Common plankton
<i>Myxococcoides</i> spp.	—	Abundant plankton
<i>Glenobotrydion aenigmatis</i> Schopf	7–12 (9.2)	Common plankton
Unnamed Form B of Knoll (1983)	75–210 (145)	Common plankton
<i>Eomycetopsis robusta</i> Schopf emend. Knoll and Golubic	—	Rare fragmented specimens; allochthonous
Filament clusters (<i>Eomycetopsis</i> sp.)	3–4	Common, allochthonous
<i>Siphonophycus kestron</i> Schopf	—	Rare, fragmented specimens, allochthonous
III. Vase-Shaped Microfossil Assemblage		
Vase-shaped Microfossils	34–257 $\times$ 16–119 (106 $\times$ 50.5)	Abundant planktonic Heterotrophs
<i>Kildinella hyperborea</i> Timofeev	—	Rare plankton
<i>Myxococcoides</i> spp.	—	Rare, allochthonous (plankton?)
<i>Eomycetopsis robusta</i> Schopf emend. Knoll and Golubic	—	Some allochthonous, some <i>in situ</i> benthos
<i>Siphonophycus kestron</i> Schopf	—	Rare, allochthonous

Late Riphean acritarchs also occur in the underlying Hunnberg Formation (Knoll 1982a), and superjacent Gotia mudstones contain scattered Vendian microfossils, thus corroborating the age assignment for the Ryssö Formation. Further corroboration comes from biostratigraphic comparison to the Eleonore Bay and Tillite Groups of East Greenland. The lithological similarities between these rocks and the Precambrian Hecla Hoek sequence of eastern Spitsbergen and Nordaustlandet were early recognized by Koch (1929) and Kulling (1934). Acritarch assemblages described by Vidal (1979) from various horizons throughout the Greenland succession correspond closely to those found in the various formations of the Murchisonfjorden Supergroup (Knoll 1982b).

Of particular interest here is Vidal's report of a diverse suite of Late Riphean acritarchs, including vase-shaped microfossils, from the upper Limestone-Dolomite 'Series' of Ella Ø and the adjacent coast. This supports Harland and Gayer's (1972) suggestion that eastern Svalbard and East Greenland were situated along a contiguous eastern North American continental margin in late Precambrian times, and adds strength to the latest Riphean age assignment for the Ryssö Formation.

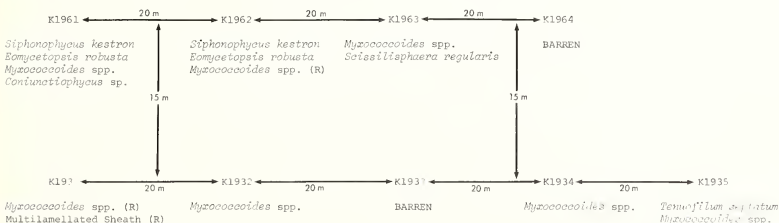
MICROFOSSIL ASSEMBLAGES

Stromatolitic microfossils. In general aspect, the stromatolitic microfossil assemblages of the Ryssö Formation are similar to those described from the Bitter Springs, Draken, and other formations of comparable age and palaeoenvironmental setting. Like the Bitter Springs biota, Ryssö assemblages are found within silicified portions of flat, cryptalgal laminated dolomites. Laminae are wavy and irregular. Commonly, a few millimetres to more than a centimetre thick layer of sand- to angular gravel-sized clastic material separates two mat horizons. The clasts themselves consist of locally derived stromatolitic dolomite or chert. Chert occurs as irregular patches to more or less continuous beds 2 to 15 cm thick. The secondary nature of the silica is indicated by the fact that chert distribution does not conform to bedding; bedding planes commonly cross lithological boundaries. There is no evidence for evaporites, and desiccation cracks are rare. Deposition apparently took place on a very shallow carbonate flat subjected to occasional storms. Early diagenetic silicification insured the long-term preservation of microfossils and amorphous organic matter.

A single horizon of densely matted *Eomycetopsis robusta* filaments is found near the top of the formation (Locality K 1924; text-figs. 1 and 2). All other stromatolitic microfossils are confined to a single thin unit near the formation's base (Localities K 1931–1935, K 1961–1963, K 2035, and K 2036; text-figs. 1 and 2).

The preservational variability and (in part related) apparent biological heterogeneity of closely spaced samples of Ryssö chert is noteworthy. Text-fig. 3 shows schematically the distribution of microfossils within a grid of samples taken at 20 m intervals along two bedding horizons separated by 15 m of intervening section. All nine samples are comparable in petrology and sedimentary structure, yet several are barren while others contain abundant and well-preserved fossils belonging to as many as four distinct species. Species composition changes from sample to sample. Interestingly, microfossils from the same stratigraphic level exposed 5 km south of the sample grid do not differ significantly from those contained in grid cherts. Such local biological and preservational heterogeneity is not surprising in the light of previous studies of microfossil distribution within the Bitter Springs (Knoll 1981) and Draken (Knoll 1982a) formations, but it counsels care in the construction of sampling strategies for Proterozoic stromatolitic cherts.

Where the remains of mat building microbes are preserved, the builders are densely interwoven populations of the 8–15 µm diameter tubular sheath *Siphonophycus kestron* Schopf (Pl. 58, figs. 4–6) and/or the somewhat thinner (2–4 µm) sheath *Eomycetopsis robusta* Schopf emend. Knoll and



TEXT-FIG. 3. Diagram showing the sampling grid and microfossil assemblages for a suite of closely spaced chert samples collected from the Ryssö Formation on Söre Russöya.

Golubic (Pl. 57, figs. 1, 4, 5). Both are interpreted as the evacuated extracellular sheaths of oscillatorian cyanobacteria. Some horizons consist exclusively of one species or the other, while at other levels, the two blue-greens occur together. This suggests that the two species had distinct microecological preferences and tolerances, but that their tolerance ranges overlapped. In modern microbial mats, it has sometimes been observed that two or more cyanobacterial species will participate in mat building under normal conditions, but should local environmental conditions change temporarily, growth of one species will increase at the expense of the other (Golubic 1973). This represents one of several ways in which individual horizons within a single stromatolite can be dominated by one or another species, or a bispecific association of the two taxa (Golubic 1973, 1976b). *Siphonophycus* and *Eomycetopsis* species have been recognized as primary or auxiliary mat builders in a number of Proterozoic stromatolitic biotas (e.g. Knoll 1981, 1982a; Zhang 1981; Mendelson and Schopf 1982). In Ryssö sample RO-MB, *E. robusta* also occurs in oncolites (see also Schopf *et al.* 1973).

Only two other filamentous microfossil species have been found in the Ryssö biota. A densely interwoven population of 1 μm thick tubular sheaths assignable to *Tenuofilum septatum* Schopf was observed in a single lamina in sample K 1935 (Pl. 57, fig. 2), and a single large (39 μm diameter) multilamellar sheath occurs within a rip-up clast in sample K 1931 (Pl. 57, fig. 6).

Mat-dwelling microbes are not widely preserved in Ryssö cherts, but in sample K 1961, irregular colonies of small (average dimension = $3.1 \times 2.3 \mu\text{m}$; $N = 100$) psilate unicells assigned to *Coniunctiophycus* sp. occur at more or less regular intervals in some bedding planes. Individual cell clusters contain two dozen to several hundred specimens; colonies are spaced 50 to 800 μm apart, with an average intercolony lateral distance of approximately 150 μm . Many of the colonies are relatively simple framboidal aggregations (Pl. 58, fig. 2), but several large colonies contain numerous simple aggregations apparently originally set in copious mucilage (Pl. 58, figs. 1, 3). Zhang's (1981) interpretation of *Coniunctiophycus* colonies as chroococcalean blue-greens is tentatively accepted here, but in truth, a bacterial interpretation for this population cannot be dismissed.

More certain are the taxonomic affinities of another benthic population. In samples K 1963, K 2035, and K 2036, large numbers of ensheathed unicells and fairly regular colonies occur in some laminae (Pl. 59, text-fig. 4). The unicells consist of rounded extracellular envelopes 11 to 45 μm in diameter which usually contain partially collapsed cellular material. Colonies are clearly large unicells that have undergone successive binary fissions (without intervening growth) in three planes to produce a regular spherical colony of 4, 8, 16, 32, or, rarely, 64 cells, all of which are preserved as individual envelopes. Occasionally, larger cuboidal colonies of more than 100 cells are found. In all cases, the retention of extracellular envelopes secreted by daughter cells following *each* successive fission preserves the divisional pattern characteristic of the species. As discussed more fully in the Systematic Palaeontology section, this population, given the name *Scissilisphaera regularis* gen. et sp.

EXPLANATION OF PLATE 57

For each figure, thin section number, stage co-ordinates (where 'x' on slide K2023-1F = 1.9×120.2), and Harvard University Paleobotanical Collection number are given. Bar in Fig. 8 = 50 μm for Figs. 1, 2, 6, and 8, and = 20 μm for Figs. 3-5, 7, 9, and 10.

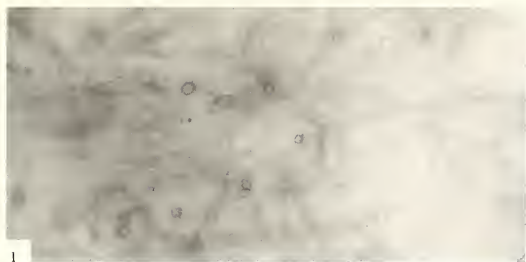
Figs. 1, 3-5. *Eomycetopsis robusta* Schopf emend. Knoll and Golubic. 1, matted population, K2035-3N, 8.6×101.5 , H.U. No. 60616. 3, filament cluster (note borders of clast), K2035-3I, 17.4×125.4 , H.U. No. 60617. 4, K1962A-1B, 8.5×122.1 , H.U. No. 60611. 5, K1962A-1B, 12.6×123.1 , H.U. No. 60612.

Fig. 2. *Tenuofilum septatum* Schopf. Densely interwoven population. K1935-1A, 6.5×103.3 , H.U. No. 60615.

Fig. 6. Multilamellated sheath. K1931-2A, 12.8×127.8 , H.U. No. 60614.

Figs. 7, 8, and 10. *Myxococcoides* sp. 7, K1963-1A, 19.8×118 , H.U. No. 60618. 8, lower power photograph of population that includes 7, showing spatial distribution of individuals. 10, K2035-1A, 18.2×128 , H.U. No. 60622.

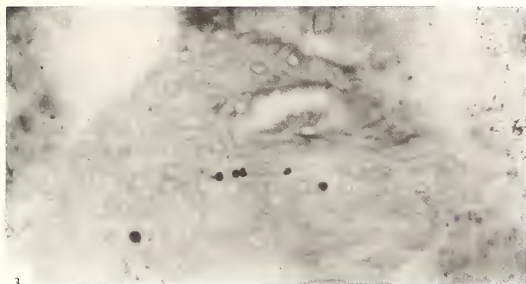
Fig. 9. *Glenobotrydion aenigmatis* Schopf. K2035-3A, 13.2×125.2 , H.U. No. 60623.



1



2



3



6



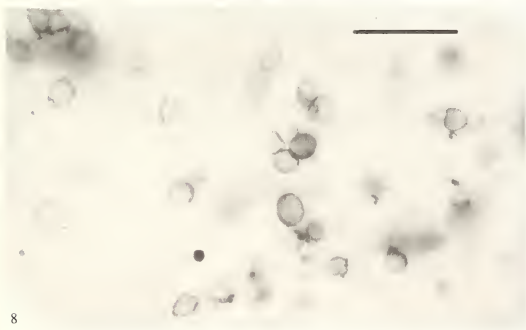
7



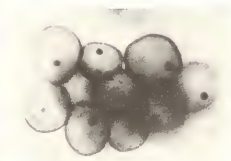
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5



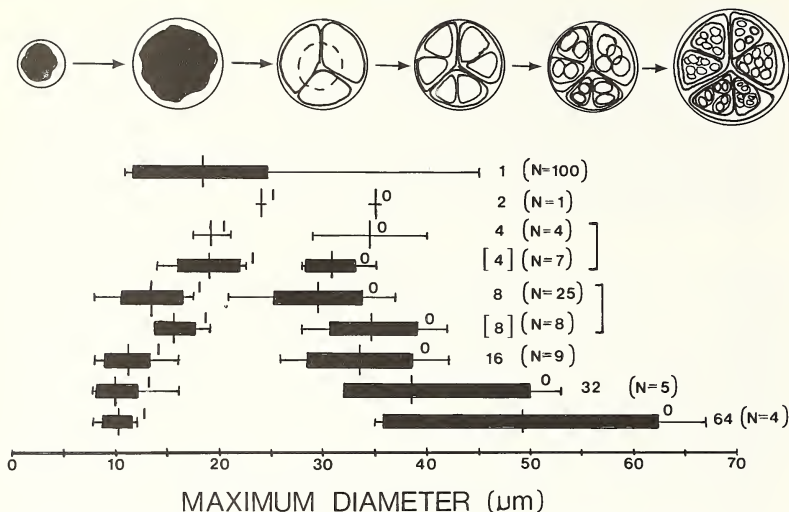
8



9



10



TEXT-FIG. 4. Size distribution of unicells and cells within colonies of *Scissilisphaera regularis* gen. et sp. nov. Thin lines indicate total size range; thick blocks extend one standard deviation above and below the mean diameter, which is indicated by the vertical line. Statistics are provided for individual unicells [1]; overall diameter [0] and diameters of individual cells for two-cell colonies [2], quartets [4], octads [8], sixteen-cell colonies [16], thirty-two cell colonies [32], and sixty-four cell colonies [64]; and for four-cell [(4)] and eight-cell [(8)] divisions that remain observable within colonies that later continued to divide. The growth and divisional cycle of *S. regularis* is diagrammed above the size distributions.

nov., is comparable in all salient features to members of the modern cyanobacterial family Pleurocapsaceae.

Planktonic microfossils. Simple spheroidal unicells assignable to the genus *Myxococcoides* are scattered throughout the stromatolitic cherts (Pl. 57, figs. 7, 8, 10; Pl. 60, fig. 14). Their wide range of size and wall thickness suggests that several species are represented, and their irregular distribution in the cherts further suggests that they are allochthonous elements, perhaps near-shore phytoplankton that dropped into and were preserved with the mats. Large planktonic acritarchs comparable to those commonly isolated from open shelf detrital rocks have been found only in a single horizon near the base of the Ryssö Formation. The locality in question (K 2035, text-fig. 1) consists predominantly of flat microbially laminated dolomites with lenses and irregular patches of black chert, some of which contain stromatolitic microfossil populations. Chert and limestone pebble conglomerates and gravel stones occur within shallow channels in the carbonates, and it is in the conglomerates that the large planktonic microfossils are found.

Petrographically, the fossiliferous rocks consist of moderately well rounded clasts of micrite 1×1 to 14×4 mm in size, along with carbonaceous chert pebbles up to 40 mm long, both set in a matrix of what was originally an organic rich carbonate. Although still preserved as dolomite in places, the matrix has largely been replaced by silica. Some relatively angular chert pebbles themselves consist of sand- to gravel-sized silica-cemented chert clasts. The channel fill thus appears to have

originated as lime muds and sands, in part organic rich, that were ripped up and redeposited in channels. Between episodes of conglomerate deposition, carbonaceous lime muds draped the accumulated pebbles and gravel. Silicification occurred early in diagenesis and was incomplete; the compound clast-in-clast nature of some pebbles demonstrates that materials were sometimes reworked more than once.

Siliceous clasts in the carbonate are always carbonaceous, while associated limestone pebbles are almost invariably devoid of organic matter. This circumstance prompts the suggestion that chert was preferentially precipitated in carbonaceous sediments. A chemical hypothesis advanced by Leo and Barghoorn (1976) to explain the silicification of wood may also explain the close relationship between chert and organic matter in Proterozoic carbonates. Leo and Barghoorn proposed that functional groups, particularly hydroxyl groups, in partially degraded wood form hydrogen bonds with dissolved monosilicic or polysilicic acid in ambient ground water. As silicic acid molecules build up, they begin to polymerize, with the expulsion of water. In this way, both the exquisite preservation of some petrified woods and the intimate relationship of silica and organic matter in petrifications are explained. Similar features in the fossiliferous Ryssö cherts (and other stromatolitic microbiotas) may best be explained by invoking analogous geochemical processes in Precambrian microbial mat sediments.

Although the conglomerates under consideration occur within a stromatolitic carbonate succession, clasts containing populations of interwoven mat filaments are rare (Pl. 57, fig. 3). Most clasts are not laminated. Conglomeratic chert pebbles do contain fossil cells, sheaths, mucilage, and indeterminate organic particles which are closely crowded together. Microfossils are more or less randomly distributed within clasts, in silicified areas of the matrix, in clasts-within-clasts, and, occasionally, in the silicified spaces between clasts in compound conglomeratic pebbles. Evidently, some fossils dropped into accumulating organic rich muds and were transported within clasts to the site of deposition, while other specimens were carried directly into the channel by transporting currents.

Twelve distinct types of large, robust-walled microfossils (acritarchs) have been identified in this assemblage (Pl. 58, figs. 7-9; Pl. 60; Table 1). Smaller spheroidal unicells also occur in abundance. Most of these smaller microfossils can be accommodated within the genus *Myxococcoides*, a form genus covering small, morphologically simple single-walled vesicles; however, it is clear that several biological species are present. Based on size-frequency distribution, characteristic clustering patterns, vesicle thickness, and the presence or absence of extracellular mucilage, most populations can be related to the previously described species *M. minor* Schopf, *M. inornata* Schopf, and *M. cantabrigiensis* Knoll. A few populations containing internal organic blebs are assigned to *Glenobrydion aenigmatis* Schopf, although it is not clear that these differ biologically from certain *Myxococcoides* populations. Rare fragments of *Eomycetopsis robusta* and *Siphonophycus kestron* sheaths occur and are considered to be allochthonous.

Among previously described silicified Precambrian microbiotas, assemblages preserved in the underlying Hunnberg Formation (Knoll 1983) compare most closely with this Ryssö florule. The Hunnberg biota includes three phytoplankton assemblages: a taxonomically depauperate lagoonal association, an open coastal shelf assemblage containing more than two dozen morphologically diverse taxa, and, within intercolumnar spaces in stromatolite bioherms that separate the first two facies, a third assemblage of intermediate character. The intermediate Hunnberg biota, representing very near shore, but none the less approximately normal marine conditions, is most similar to the Ryssö assemblage under consideration. Both assemblages are dominated by *Chuarina circularis* Walcott and Unnamed Form B of Knoll (1983), and several other taxa are found in common. The Ryssö microbiota differs from known Hunnberg assemblages in that it contains the large and distinctive fossil *PterospERMOSIMORPHA* sp. (Pl. 58, figs. 7, 8) and *Trachysphaeridium lauffeldi* (Pl. 60, figs. 1, 2). The presence of these forms in the younger but not the older biota may indicate an evolutionary first appearance, but environmental factors and chance cannot be ruled out as causes of microfloral differences. In general, the Ryssö acritarch florule is more similar to assemblages described from Precambrian siltstones and shales than it is to silicified microbiotas.

Biologically, the affinities of most of these fossils are uncertain. Large, robust-walled acritarchs are generally considered to be the reproductive cysts of eukaryotic phytoplankton (see discussions in Downie 1973 and Vidal and Knoll 1983); however, the algal division or divisions represented are unclear. Much opinion favours a green algal relationship for Precambrian sphaeromorphs, by comparison to the large cysts of the modern green flagellates, the prasinophytes; but at the moment such inferences remain conjectural. The stratigraphic import of these microfossils is more certain. Late Precambrian and Cambrian acritarch assemblages show clear evolutionary trends, and a number of assemblage zones have been recognized and used to correlate strata on an intercontinental basis (Vidal 1981*b*; Vidal and Knoll 1983). The Late Riphean character of the Ryssö biota demonstrates that even the local occurrence of planktonic microfossils can allow accurate biostratigraphic placement of an Upper Proterozoic succession.

Vase-shaped microfossils. In the upper third of the Ryssö Formation, acritarchs and cyanobacterial microbenthos are rare, occurring only as scattered and, in general, poorly preserved individuals. Flask- or vase-shaped microfossils (VSM's), on the other hand, occur in great abundance (Pl. 61).

A few, apparently washed-in, VSM's can be found in silicified patches within platy bedded, crinkly laminated dolomites near the top of the formation (samples K 1929, K 1931). These carbonates record very shallow, near shore marine conditions. Much larger VSM populations occur in a stratigraphically lower sequence dominated by pyritic black shales (samples K 1970-2, K 1981, K 13322). In this succession, bituminous micrite beds a few centimetres to 1.5 m thick occur at several metre intervals within some 30 m of fissile, organic-rich shales. In some horizons, the carbonates have been almost entirely replaced by silica, but more commonly chert occurs as oblong concretions a few centimetres thick within the limestone. This sequence appears to have been deposited in a local basin characterized by restricted bottom circulation. VSM's have been recognized in macerations of bituminous limestone and shale samples, but they are most easily studied in petrographic thin sections of chert.

Petrographically, the fossiliferous cherts consist of a mosaic of extremely small quartz crystals ($< 10 \mu\text{m}$ in diameter). Carbonate replacement tends to be incomplete, with small, etched grains persisting throughout the matrix. Late-stage diagenetic rhombs of dolomite occur sporadically throughout the samples studied, and these truncate both quartz crystallization patterns and, occasionally, microfossils (Pl. 61, figs. 2, 9). The cherts are richly carbonaceous. Amorphous organic debris is distributed in closely spaced, discontinuous organic lamellae, as well as in continuous layers up to $100 \mu\text{m}$ thick.

VSM's occur as organically preserved fossils and, more commonly, as casts. Casts are filled by single large crystals of carbonate conforming to the shape of the original organism, by silica, or by some combination of the two minerals. Where carbonate and chert co-occur, the carbonate crystals are often markedly etched, indicating the diagenetic sequence of mineralization. Chert often is in the

EXPLANATION OF PLATE 58

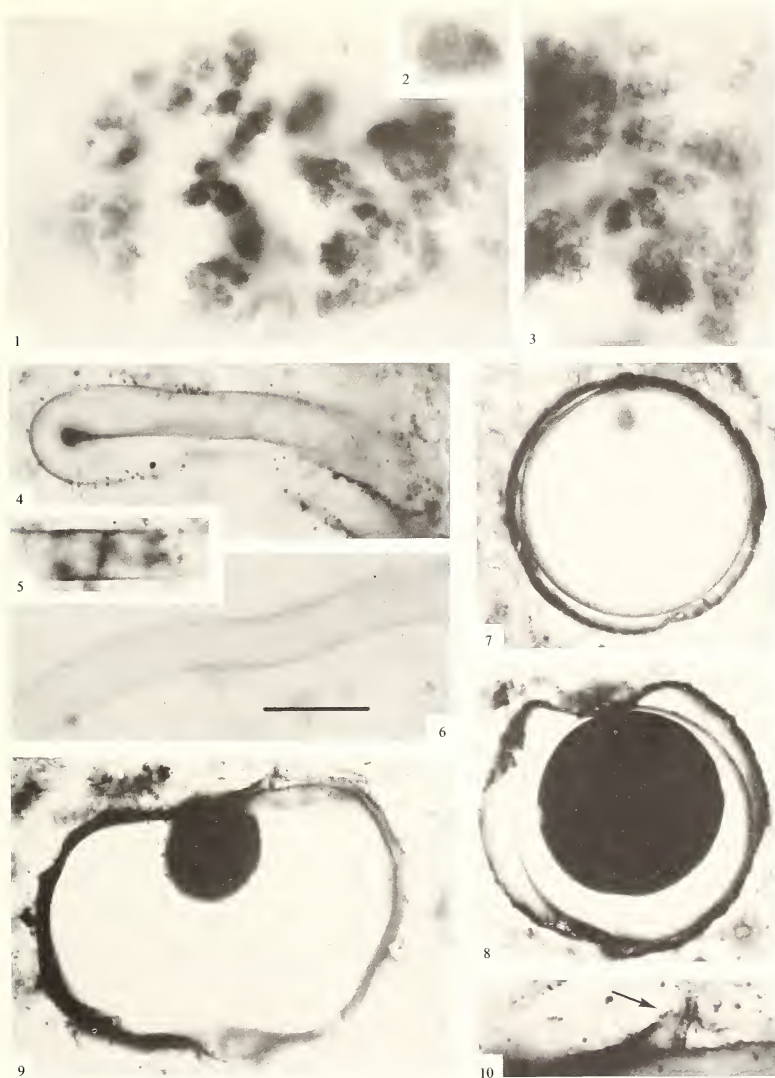
For each figure, thin section number, stage co-ordinates (where 'x' on slide K2023-1F = 1.9×120.2), and Harvard University Paleobotanical Collection number are given. Bar in Fig. 6 = $25 \mu\text{m}$ for Fig. 1; = $20 \mu\text{m}$ for Figs. 2-6, and 10; = $60 \mu\text{m}$ for Figs. 7 and 8; and = $70 \mu\text{m}$ for Fig. 9.

Figs. 1-3. *Coniunctophycus* sp. 1, large colony, K1963-1A, 23.5×102 , H.U. No. 60631. 2, small cluster, K1963-10, 18×110 , H.U. No. 60632. 3, details of colony shown in 1.

Figs. 4-6. *Siphonophycus kestoni* Schopf. 4, 1962-1B, 20.2×130.6 , H.U. No. 60607. 5, K2035-3E, 18.5×110.3 , H.U. No. 60608. 6, K1962A-1B, 9.1×111.6 , H.U. No. 60609. Note apparent septation in 5.

Figs. 7 and 8. *Pterospirifer* sp. 7, K2035-3E, 8.6×120.7 , H.U. No. 60633. 8, K2035-3E, 12.1×111.8 , H.U. No. 60634.

Figs. 9 and 10. *Trachystrichosphaera vidalii* Knoll. 9, K2035-3M, 8.2×118.3 , H.U. No. 60635. 10, detail of 9. Arrows point to characteristic columnar processes.



KNOLL and CALDER, Late Precambrian microbiotas

form of fibrous chalcedony, radiating inward from cast walls. It is likely that at least in some cases, silica was precipitated in a microscopic cavity within the organic structure, rather than as a replacement of pre-existing carbonate. Chert in VSM casts can also occur as more or less equant crystals. In these cases, crystal size is notably larger than in the surrounding matrix and there is always a mineral discontinuity at microfossil boundaries; i.e. chert crystals do not transgress fossil walls whether these be organically preserved or defined by casts. In summary, petrographic evidence suggests that VSM's accumulated in anoxic carbonaceous micrites during Ryssö times. After decomposition of any internal cellular material, many skeletons were filled with carbonate, while others remained empty. Subsequent to the partial or total degradation of the walls themselves, the VSM-bearing sediments became silicified. Internal void spaces were filled and carbonate casts were, for the most part, partially or completely replaced by silica. Casts are often draped in amorphous organic matter, further accentuating their morphology (Pl. 61, figs. 7, 13).

TABLE 2. Dimensions of vase-shaped microfossils in the Ryssö Formation

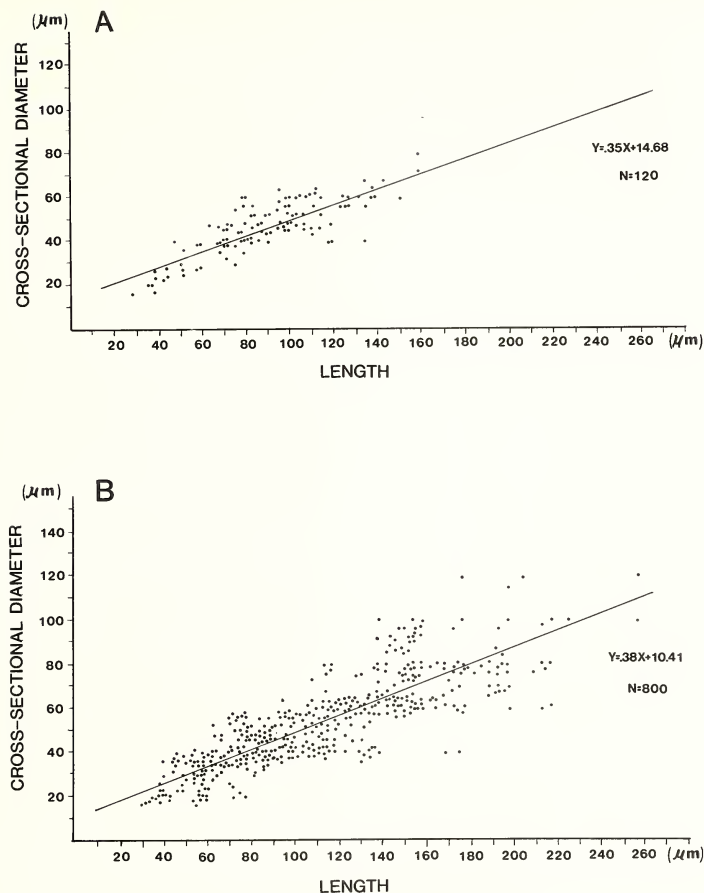
	Length (μm)			Maximum cross-sectional diameter (μm)		
	Range	Mean	Standard deviation	Range	Mean	Standard deviation
All VSM's ($N = 920$)	34-257	106	38	16-119	50.5	16
Organically preserved VSM's ($N = 120$)	34-158	90	27	16-79	46	12
VSM casts ($N = 800$)	78-257	108	39	16-119	51	16

Linear regression equations for length, L, versus diameter, D. (Reduced major axis.)

All VSM's	$D = 0.36 L + 12.4$ ($r = 0.80$)
Organically preserved VSM's	$D = 0.35 L + 14.7$ ($r = 0.80$)
VSM casts	$D = 0.38 L + 10.4$ ($r = 0.82$)

Morphologically, the VSM's are elongate ovoid to pear-shaped bodies, broadly rounded at the base and gradually tapering to an aperturate apex. The aperture may appear as a simple circular truncation of the vesicle or it may be surrounded by a distinct collar region. Dimensions for a sample population are given in Table 2, as are reduced major axis linear regression equations for length vs. maximum cross-sectional diameter. Size distribution is displayed graphically in text-fig. 5. It is interesting to note that organically preserved VSM's have a much more limited size range than do casts. Specifically, very large casts have no counterpart among organic tests. This is in spite of the facts that the regression equations for the two subpopulations are nearly identical (slopes not significantly different at the 5% level, as determined by use of the Z statistic) and that the two preservational forms occur together in the same beds, often in the same microhorizons. Whether the organic and cast populations represent one species or two is unclear, although a taphonomic explanation for the preferential retention of organic walls in small specimens is considered likely.

Precambrian VSM's were first described by Ewetz (1933) from silicified phosphate nodules of the Upper Riphean to lower Vendian (*sensu* Vidal 1976) Visingsö Beds, Sweden. Bloeser *et al.* (1977) discovered large populations of organically preserved VSM's in carbonaceous shales and (rarely) in cherty pisolite beds of the Upper Riphean Kwagunt Formation exposed in the Grand Canyon, Arizona. The Kwagunt specimens were initially divided into 'flask-shaped' and 'tear-shaped' morphotypes, the latter being longer and narrower. Lengths ranged from 48 to 145 μm ($\bar{x} = 96 \mu\text{m}$, $s = 20 \mu\text{m}$, $N = 90$). Bloeser (1980) has considered that several species can be differentiated on the basis of collar morphology. The Ryssö VSM population, especially the organically preserved subpopulation, is morphologically similar to the Grand Canyon VSM assemblage. Svalbard tests are on the average more elongate than those from Arizona (length to width ratios are 2.1:1 and 1.4 to 1.7:1, respectively), but the entire range of flask- and tear-shaped morphologies reported by Bloeser



TEXT-FIG. 5. Bivariate plots of size distribution for vase-shaped microfossils in the Ryssö Formation. A, organically preserved individuals. B, specimens preserved as casts. Lines indicate reduced major axis regression lines relating length and width.

et al. (1977) can be found in the Ryssö Formation. Bloeser *et al.* (1977) and Bloeser (1980) also reported the presence of opercula plugging the apical openings of Kwagunt VSM's. We have not observed any opercula in Ryssö microfossils, although the complete absence of organically tinted sedimentary matrix from VSM interiors might be advanced as an indirect argument for the former

presence of an opercular structure. Because the details of collar morphology are rarely well defined in the Ryssö population, we are unable to subdivide the Svalbard populations by Bloeser's criteria; however, the points of similarity between the two populations are such that we regard them as representing closely related micro-organisms.

In the wake of Bloeser *et al.*'s (1977) initial paper on these distinctive microfossils, VSM's have been discovered in a number of late Precambrian deposits. Fairchild *et al.* (1978) reported VSM's 16 to 120 μm long from limestone cobbles in conglomerates of the Urucum Formation of south-western Brazil. Additional specimens were found in shallow marine dolomites from Jabal Rokham, Saudi Arabia, a sequence that has been correlated with the 638 to 600 Ma Murdama Group (Binda and Bokhari 1980). Knoll and Vidal (1980) described large new populations of VSM casts from phosphate nodules in silty argillites and siltstones of the upper Visingsö Beds, Sweden. Sizes in this population range from 60 to 130 $\mu\text{m} \times 25$ to 62 μm ; average dimensions equal $98 \times 52 \mu\text{m}$ for $N = 300$. Finally, VSM's have been reported from several carbonate units thought to be depositionally related to the Ryssö Formation. Abundant specimens occur in the Backlundtoppen and Draken Conglomerate formations of Ny Friesland, Svalbard (Knoll 1981, and unpublished data), and other populations are found in the Limestone-Dolomite 'Series' of the upper Eleonore Bay Group, East Greenland (Vidal 1979).

The wide facies distribution of VSM's suggests that they are the remains of planktonic micro-organisms. Morphologically, VSM's are not closely comparable to unicellular algae, but they are quite similar to protozoans of several types. Bloeser *et al.* (1977) originally described the Grand Canyon VSM's as probable chitinozoans, stressing the morphological resemblance between the Precambrian fossils and members of the Ordovician-Silurian chitinozoan genus *Desmochitina*. In a more conservative assessment, Bloeser (1980) later classified them as microfossils *incertae sedis*.

Fairchild *et al.* (1978) suggested protistan affinities for the Brazilian VSM population, specifically citing the ciliate Tintinnida. Other amoeboid and ciliate protists build organic loricas similar in size and shape to VSM's; however, tintinnids make an intriguing comparison for several reasons. Ecologically, tintinnids are marine, pelagic protists that can be among the most important micropredators in coastal ecosystems. They form robust pseudochitinous tests similar to those of VSM's. In VSM's, the basal region is preferentially preserved relative to the collar, a phenomenon also recorded for modern tintinnids. Tappan and Loeblich (1968) noted differences in wall characteristics of base and collar regions of *Codonellopsis*, a modern vase-shaped ciliate protist; the long and very delicate collar region is solely organic and is, hence, less resistant to post-mortem degradation, while the solidly constructed base of the lorica consists of a combination of secreted and agglutinated materials and is therefore much more likely to be preserved.

Reid and John (1981) recently examined reproductive cysts of modern tintinnids. These bodies are vase-shaped, collared, and operculate. The resemblance to some morphologically simple chitinozoans prompted Reid and John to conjecture that certain chitinozoans may be tintinnid cysts. A cyst explanation for the Ryssö VSM populations merits consideration although it cannot be demonstrated to the exclusion of other hypotheses.

It seems, therefore, that at present it is impossible to ascertain unequivocally the exact biological affinities of Precambrian VSM's; however, we reiterate the conclusion of Knoll and Vidal (1980) that the organisms preserved as VSM's were most likely heterotrophic protists, similar in general ecological role to the modern Tintinnida.

DISCUSSION

The record of latest Riphean coastal marine life revealed by the Ryssö biotas is far from complete. Processes of fossilization strongly constrain our views of ancient life, limiting our vision to the microbiotas of selected environments in which post-mortem degradation was arrested at an early stage. Within those biotas, species differentially resistant to decomposition were selectively preserved, and even within individual organisms, those *parts* of the organisms most resistant to post-mortem

degradation were preferentially incorporated into the record. One might think that the record that has survived would seem depressingly impoverished, but that is in fact not the case. On the contrary, preserved Ryssö assemblages suggest that a taxonomically and ecologically diverse microbiota thrived along the Svalbard coast 800 to 700 Ma ago. Stromatolites are widely distributed in the Ryssö Formation, indicating that microbial mats covered much of the shallow Ryssö sea floor. The heterogeneity of the stromatolite morphologies and microstructures implies a concomitant heterogeneity in the microbial communities responsible for mat accretion. Only a single stromatolite type is represented by a preserved microbiota, but this assemblage reveals heterogeneity in both cyanobacterial mat builders (three different builders occurring singly or in combination) and in mat dwelling micro-organisms (0 to 2 preserved dwellers in mats). This is not unexpected in view of the impressive diversity of mat associations present in other flat laminated stromatolites of comparable age (Knoll 1981, 1982a).

The shallow and perhaps somewhat restricted seas that periodically inundated the broad Ryssö carbonate flats had a limited plankton biota. The small allochthonous unicells associated with some Ryssö stromatolitic microbiotas are interpreted as inshore phytoplankton or periphyton. The taxonomic affinities of these cells are uncertain, although at least some of them may have been eukaryotic algae. Eukaryotic phytoplankters that produced large, robust, morphologically complex reproductive cysts thrived in more open coastal waters. Again, this 'lateral' distribution of plankton types is not unique to the Ryssö Formation. It appears to be as characteristic of late Precambrian phytoplankton as it is of Phanerozoic algae (Vidal 1976; Knoll 1983; Vidal and Knoll 1983).

Ecological and environmental differences (modified by the effects of disturbance and chance colonization) thus provide a satisfying explanation for the distribution of phytoplankton and stromatolitic microbenthos in the Ryssö Formation, but what of the VSM's? These organisms were probably micropredators and so must have coexisted with phytoplankton populations, yet where VSM's are abundant, other organisms are rare or absent and vice versa. The key to this distributional problem may lie in fossil preservation. To our knowledge, the best preserved organic tests of VSM's are found in organic-poor carbonates and cherts. The chemical composition of these tests is unknown, but it may be such that early diagenetic conditions inimical to the preservation of most algae and cyanobacteria have little effect on VSM's. Conversely, good conditions for algal and blue-green fossilization may promote the dissolution of VSM tests. Therefore, the segregation of VSM populations as a distinct assemblage type may be associated with taphonomy and only indirectly reflect the ecological distribution of the living organisms.

In summary, the biota of the latest Riphean Ryssö coastal seaway included a variety of essentially prokaryotic microbial mat communities distributed across the intertidal to shallow subtidal carbonate flats. Cyanobacteria constitute the best preserved members of these communities, but the mats undoubtedly also contained a host of metabolically diverse aerobic and anaerobic, photosynthetic and heterotrophic bacteria. The benthos may also have included eukaryotic algae and simple seaweeds, although such organisms are not preserved in the Ryssö Formation. A diverse, eukaryote dominated phytoplankton biota lived in the water column above open coastal sediments, but in more restricted inshore waters only a depauperate assemblage of simple unicells thrived. Heterotrophic protists capable of micropredation were an integral part of coastal food webs. The Ryssö Formation thus provides an unusually clear picture of the complexity of microbial life just prior to the initial radiation of metazoans.

SYSTEMATIC PALAEOLOGY

All specimens come from exposures of the Upper Riphean Ryssö Formation in the vicinity of Murchisonfjorden, Nordaustlandet, Svalbard. Illustrated material is housed in the Palaeobotanical Collections of Harvard University. Comparative materials are housed in the Palaeontological Museum of Oslo University. In the interests of brevity, full synonymies are not presented for each species. These can be found in the recent monographs of Vidal (1976, 1981a) and Mendelson and Schopf (1982).

Kingdom MONERA Haeckel, 1878
 Division CYANOPHYTA (Sachs) Pascher, 1931
 Class COCCOGONEAE Thuret, 1875
 Order CHROOCOCCALES Wettstein, 1924
 Family CHROOCOCCACEAE Nägeli, 1849
 Genus CONIUNCTIOPHYCUS Zhang, 1981

Type species. Coniunctiophycus gaoyuzhuangense Zhang, 1981

Coniunctiophycus sp.

Plate 58, fig. 3

Description. Spheroidal to slightly elongated organic walled vesicles; walls thin, psilate to very finely granular. Individual cells 2–9 μm long ($\bar{x} = 3.1 \mu\text{m}$, $s_x = 1.0 \mu\text{m}$, $N = 100$) and 2–6 μm wide ($\bar{y} = 2.3 \mu\text{m}$; $S_y = 0.7 \mu\text{m}$; $N = 100$); see text-fig. 6. Cells arranged in tight, irregularly spheroidal clusters 10 to 20 μm in diameter containing 50–200 cells. Cell clusters commonly occur together in botryoidal aggregates up to 200 μm in maximum diameter. Large aggregates commonly give the appearance of growth inward into a cavity from cell populations lining the cavity walls. No external mucilage is apparent, but the spacing of clusters within the large aggregates suggests that some mucilage was originally present. Cell contents generally absent. Cell division apparently occurred by repeated binary fissions.

Discussion. Zhang (1981) erected the genus *Coniunctiophycus* for small spheroidal unicells clustered into ellipsoidal to spheroidal colonies, which, in turn, were aggregated into larger colonies. From fossil assemblages in the 1500–1400 Ma Gaoyuzhuang Formation, China, he described two species belonging to this genus: *C. gaoyuzhuangense* (average diameter = 4.0 μm) and the distinctly smaller *C. conglobatum* (average diameter = 1.4 μm). The Ryssö populations in question clearly fall within the limits of the genus *Coniunctiophycus*, but fall midway in size between the two described species. For this reason, we have elected to refer to the Svalbard fossils as *Coniunctiophycus* sp.

Among modern cyanobacteria, a number of coccoidal genera can produce colonies resembling *Coniunctiophycus*. A cyanobacterial interpretation for these fossils is accepted here, although it is acknowledged that other bacterial affinities cannot be completely ruled out.

Coniunctiophycus colonies occur in specific laminae at fairly regular intervals of 50 to 800 μm . This distribution within filamentous mats supports their interpretation as mat-dwelling microbenthos.

Order PLEUROCAPSALES Geitler, 1925
 Family PLEUROCAPSACEAE Geitler, 1925
 Genus SCISSILISPHAERA gen. nov.

Type species. Scissilisphaera regularis sp. nov.

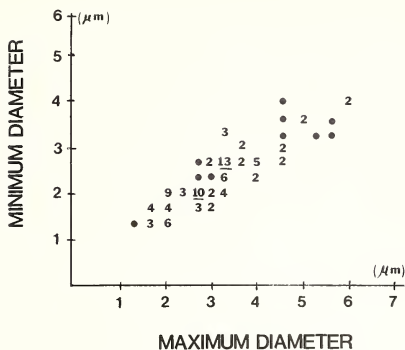
Diagnosis. Spherical to spheroidal vesicles; vesicle wall single, light, thick, and finely granular, or multilamellated. Individual vesicles sometimes containing a single, large, irregular organic body with a well-defined wall. More often, the vesicle is subdivided internally into 2, 4, or 8 smaller vesicles, each having a single wall comparable to that of the external wall. Internal vesicles often contain 2, 4, or 8 still smaller vesicles, resulting in a total of up to 64 spheroidal vesicles packed within the outer wall. Subdivided vesicle geometry reflects division in three planes. Larger aggregates form irregularly cuboidal packages of 100 or more vesicles; in these colonies the outermost vesicle wall is absent.

Etymology. From the Latin *scissilis*, meaning 'that which may be split readily', and *sphaera*, meaning 'sphere'. Thus, an easily divided sphere.

Scissilisphaera regularis sp. nov.

Plate 59

Diagnosis. Qualitatively, as for genus. Undivided vesicles 11 to 45 μm in diameter, averaging 18.2 μm .



TEXT-FIG. 6. Bivariate plot of maximum vs. minimum diameter for a sample population ($N = 102$) of *Coniunctiophycus* sp. Numbers indicate number of specimens having a given pair of dimensions. Single specimens are indicated by dots.

Small undivided vesicles may be closely packed in irregular aggregates; larger individuals are solitary or occur in loose clusters. Subdivided vesicles are generally equal in size to the largest of the undivided vesicles—for dyads, tetrads, octads, and 16-cell colonies, the diameters of the external vesicle wall are $35\ \mu\text{m}$, $34.5\ \mu\text{m}$, $29.5\ \mu\text{m}$, and $34.8\ \mu\text{m}$, respectively. Internal vesicle diameters are $24\ \mu\text{m}$, $19.2\ \mu\text{m}$, $13.5\ \mu\text{m}$, and $11.2\ \mu\text{m}$, respectively. Vesicles containing 32 or 64 small, internal vesicles are often larger (up to $70\ \mu\text{m}$), but still retain a spherical to slightly tuberosus shape. Colonies containing more than 64 subdivided units tend to be irregularly cuboidal packets.

Holotype. The specimen illustrated on the left in Pl. 59, fig. 8 has been designated the type of the species. Harvard University Botanical Collections No. 60643.

Etymology. From the Latin *regularis*, meaning 'according to a rule or pattern'. This name reflects the regular geometric pattern of cell division in this species.

Type Locality. Outcrops of Ryssö Formation exposed 2 km south of Roaldtoppen (south shore of Murchisonfjorden) in Nordaustlandet, Svalbard, near small, unnamed lake.

Description. Populations dispersed irregularly along bedding planes. Individuals consist of a spherical to spheroidal, thick, finely granular wall or a multilamellated wall. Diameter of unicells ranges from 11 to $45\ \mu\text{m}$ ($\bar{x} = 18.2\ \mu\text{m}$, $s_x = 6.4\ \mu\text{m}$, $N = 100$). Internal contents—raisin-like, folded, and wrinkled organic bodies with well-defined walls—indicate that even the largest undivided vesicles contained only a single cell. Smaller individuals often occur in tightly packed, irregular clusters, although they are sometimes found as loosely aggregated populations or as scattered solitary fossils. Larger individuals (those $> 20\ \mu\text{m}$) usually occur in loosely aggregated groups or as solitary cells. Vesicles larger than $25\ \mu\text{m}$ are often subdivided internally into 2, 4, or 8 tightly packed vesicles, each having a wall thinner than, but comparable in quality to, the outer vesicle wall. These internal vesicles, in turn, may be subdivided internally into 2, 4, or 8 smaller vesicles, resulting in spheroidal colonies of 2, 4, 8, 16, 32, or 64 cells (although the occasional failure of some vesicles to divide produces colonies whose cell number deviates from the geometric series). Size distribution for colonies of various cell numbers are presented in text-fig. 4, as is a diagram of the observed divisional sequence. Colonies of more than 64 cells are irregularly cuboidal, and are not bound by an all-encompassing vesicle wall (Pl. 60, figs. 10, 12).

Undivided unicells are the most commonly encountered form in the population. Dyads and quartets occur

infrequently, but octads are very common. Colonies of 16, 32, and 64 cells occur with decreasing frequency. In more highly subdivided colonies, the internal walls formed during the 2- and 4-cell stages are often impossible to differentiate.

Discussion. The vesicle walls described for *Scissilisphaera* are interpreted as originally closely invested extracellular envelopes—the F layer of Waterbury and Stanier (1978). The wrinkled internal bodies found in unicells and some dyads and quartets are interpreted as partially coalesced cellular remains. True cell contents are rarely preserved in subdivided vesicles. From the fossil population, one can reconstruct a divisional sequence for *Scissilisphaera*. The cycle began with relatively small (*c.* 11 μm) individuals surrounded by an extracellular envelope. Cells grew (and envelopes expanded) until they reached a diameter of approximately 30 to 45 μm (mean diameter of subdivided spheres = 32.5 μm ; $N = 50$ colonies) and then began to undergo a series of binary divisions in three planes, apparently with little or no growth between fissions. The absence of interdivision growth is attested to by the fact that large unicells, dyads, quartets, octads, and 16-cell colonies all have about the same external diameters. Colonies of 32 and 64 cells tend to be a bit larger; this may indicate resumption of growth or it may simply indicate that larger cells cleave into a greater number of small cells. After each division, a new extracellular envelope was secreted by each daughter cell. Cellular material disappeared during post-mortem degradation, but the envelopes were preserved, and their Matruschka doll arrangement of smaller sheaths inside larger ones makes it easy to reconstruct divisional patterns. At the 8, 16, 32, or 64 cell stage, the outer envelopes ruptured and the small individual cells either dispersed to begin a new cycle or resumed growth and binary fission in three planes without dispersal to produce cuboidal aggregates.

The repeated cleavage of cyanobacterial cells without intervening growth is known as multiple fission, and the small reproductive cells produced by multiple fission have been termed baeocytes (Waterbury and Stanier 1978). Using the terminology of microbiologists, one can interpret *S. regularis* as a cyanobacterium which reproduced by multiple fission to form baeocytes (equivalent to the smallest subdivisions in the spherical colonies). Among extant blue-greens, multiple fission is found only in the order Pleurocapsales, where it is the characteristic mode of reproduction (Waterbury and Stanier 1978).

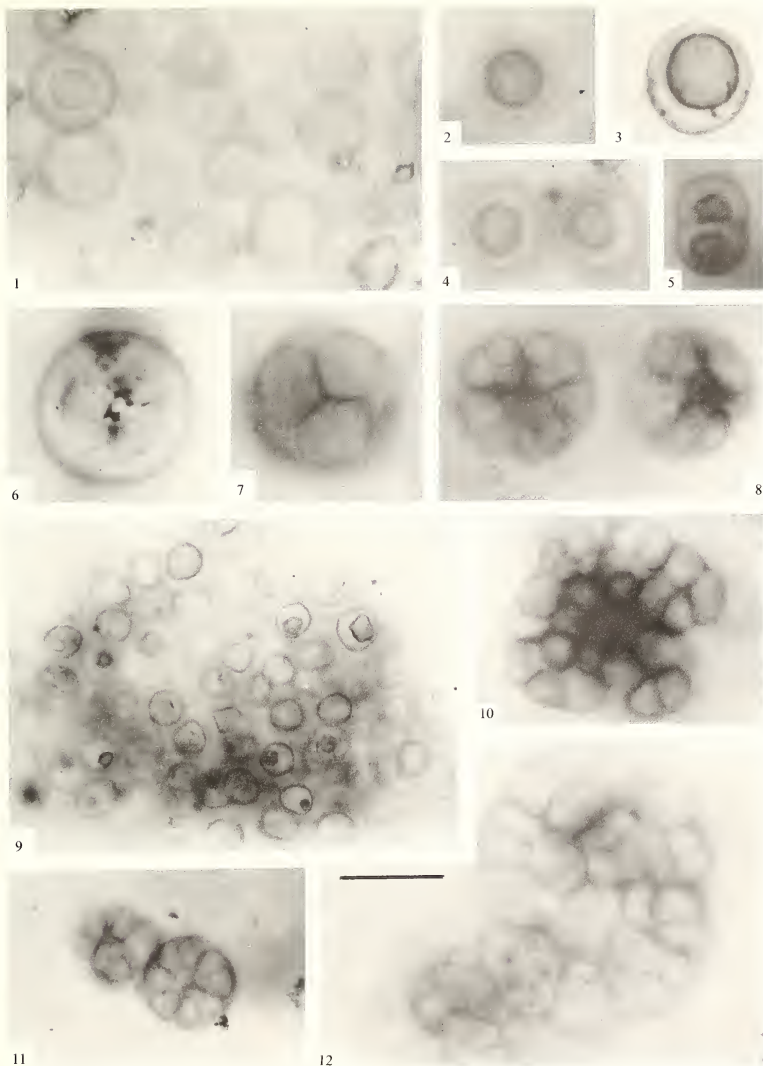
Another pleurocapsalean trait manifest in *S. regularis* is a distinctive wall structure. Members of the modern Pleurocapsales form cell walls much like other gram negative bacteria; an inner peptidoglycan layer is surrounded by an outer layer that contains lipopolysaccharides. Pleurocapsalean blue-greens, however, characteristically form a third layer (the F layer) similar in ultrastructure to the sheaths and envelopes of other blue-greens, but which closely invests the cell so that it is often difficult or impossible to detect by light microscopy of healthy populations (Waterbury and Stanier 1978). F layers do not participate in binary fission, but a new F layer is secreted by each daughter cell immediately following cleavage. The geometry of the envelopes in *S. regularis* colonies strongly suggests that they are differentially preserved F layers formed after each successive cell division.

Thus, there is little doubt that *S. regularis* belongs to the Pleurocapsales. Genera within this group

EXPLANATION OF PLATE 59

For each figure, thin section number, stage co-ordinates (where 'x' on slide K2033-1F = 1.9 $\times$ 120.2), and Harvard University Paleobotanical Collection number are given. Bar in Fig. 12 = 20 μm for Figs. 1–7; = 25 μm for Figs. 8, 10, and 12; and = 40 μm for Figs. 9 and 11.

Figs. 1–12. *Scissilisphaera regularis* gen. et sp. nov. 1, K2036-6A, 20.3 $\times$ 122.7, H.U. No. 60636. 2, K2036-6A, 4.6 $\times$ 123, H.U. No. 60637. 3, K2035-2A, 2 $\times$ 121.9, H.U. No. 60638. 4, K2036-6A, 4.6 $\times$ 123, H.U. No. 60639. 5, K2035-2A, 2.3 $\times$ 122.1, H.U. No. 60640. 6, K2035-2A, 3 $\times$ 125.6, H.U. No. 60641. 7, K2035-2A, 2.3 $\times$ 125, H.U. No. 60642. 8, K2035-2A, 2.8 $\times$ 124.6, H.U. No. 60643. 9, K2036-6A, 16.6 $\times$ 115.4, H.U. No. 60610. 10, K2035-2A, 2.2 $\times$ 123.4, H.U. No. 60647. 11, K2035-2A, 2.5 $\times$ 124.9, H.U. No. 60613, two spheroidal colonies showing nature of successive fissions within each individual colony. 12, K2035-2A, 0.9 $\times$ 114.8, H.U. No. 60649.



have been differentiated on the basis of the presence or absence of vegetative binary fissions in addition to the ubiquitous multiple fission, the geometry of colonies, and the motility (or lack thereof) of the baeocytes—apparently a function of whether or not baeocytes are invested by an F layer (Waterbury and Stanier 1978). *Scissilisphaera* is similar to the extant genus *Dermocarpa* in that individual cells grow to a large size (up to 30 μm in *Dermocarpa*) before undergoing multiple fission to form spherical colonies; however, *Dermocarpa* multiple fissions usually result in the formation of large numbers (up to several hundred) of very small baeocytes. *Dermocarpa* baeocytes are not enveloped in individual F layers, and *Dermocarpa* is incapable of forming cuboidal colonies by simple binary fissions. *Xenococcus* has F layer surrounded baeocytes, but again, does not exhibit simple binary fission.

Myxosarcina, *Chroococcidiopsis*, and the several traditionally defined genera placed by Waterbury and Stanier (1978) in the 'Pleurocapsa group' all divide by binary fission as well as multiple fission. *Pleurocapsa* group blue-greens often form pseudofilamentous outgrowths of colonies, a feature not observed in any *Scissilisphaera* populations. *Myxosarcina* and *Chroococcidiopsis* undergo binary divisions in three planes to produce cuboidal colonies, much as is seen in *Scissilisphaera*. (Compare Waterbury and Stanier 1978, Figs. 24b and 25b with Pl. 59, fig. 12.) The genera are differentiable largely by the presence of motile baeocytes in *Myxosarcina*.

Thus, in its ability to divide by both binary and multiple fission, in the apparently immotile nature of its baeocytes (as evidenced by the presence of envelopes on all cells produced by multiple fission), and in the relatively low number of baeocytes produced per parent cell (4–64), *Scissilisphaera regularis* appears most similar to living blue-greens of the genus *Chroococcidiopsis*. The large size of individual cells is not characteristic of the modern genus, nor is the segregation of vegetatively produced cuboidal packets from the loosely aggregated populations of individuals undergoing multiple fission. Perhaps the fossil chroococcidiopsis was simply larger than extant species, or perhaps the fossil species combined features that today characterize different genera. A third possibility is that more than one pleurocapsalean species is represented in the populations included in *S. regularis*—diverse pleurocapsalean species are found in modern intertidal zones. Militating against this last possibility, however, is the intimate spatial intermingling and the apparent morphological continuity between cuboidal aggregates and spherical colonies.

Several other pleurocapsalean blue-greens have been described from Proterozoic rocks. *Baylinella faveolata* (Shepeleva) Vidal (= *Sphaerocongregus variabilis* Moorman, according to Vidal 1976) was

EXPLANATION OF PLATE 60

For each figure, thin section number, stage co-ordinates (where 'x' on slide K2023-1F = 1.9 $\times$ 120.2), and Harvard University Paleobotanical Collection number are given. Bar in Fig. 6 = 40 μm for Figs. 1, 2, 7, and 13; = 50 μm for Figs. 3 and 10; = 20 μm for Figs. 4 and 5; = 120 μm for Fig. 6; = 150 μm for Figs. 8 and 9; and = 25 μm for Figs. 11, 12, and 14.

Figs. 1 and 2. *Trachysphaeridium lauffeldi* Vidal. 1, cross-section showing small, conical spines at arrow, K2035-3I, 1 $\times$ 124.6, H.U. No. 60650. 2, surface view of same specimen.

Fig. 3. *Trachysphaeridium levis* (Lopukhin) Vidal. K2035-3J, 16.5 $\times$ 126.6, H.U. No. 60651.

Figs. 4 and 5. *Trachysphaeridium* sp. A of Knoll (1983). K2035-3B, 19 $\times$ 112.4, H.U. No. 60652.

Fig. 6. Unnamed Form B of Knoll (1983). Note diagenetic wrinkling of surface K2035-3L, 17.3 $\times$ 112.3, H.U. No. 60653.

Fig. 7. *Phanerospheerops capitans* Schopf. K2035-3C, 6.5 $\times$ 103.5, H.U. No. 60673.

Fig. 8. *Trachysphaeridium* sp. B of Knoll, 1983. K2035-3H, 16.5 $\times$ 97.3, H.U. No. 60630.

Fig. 9. *Chuarina circularis* Walcott. 2035-3F, 11.5 $\times$ 113.5, H.U. No. 60628.

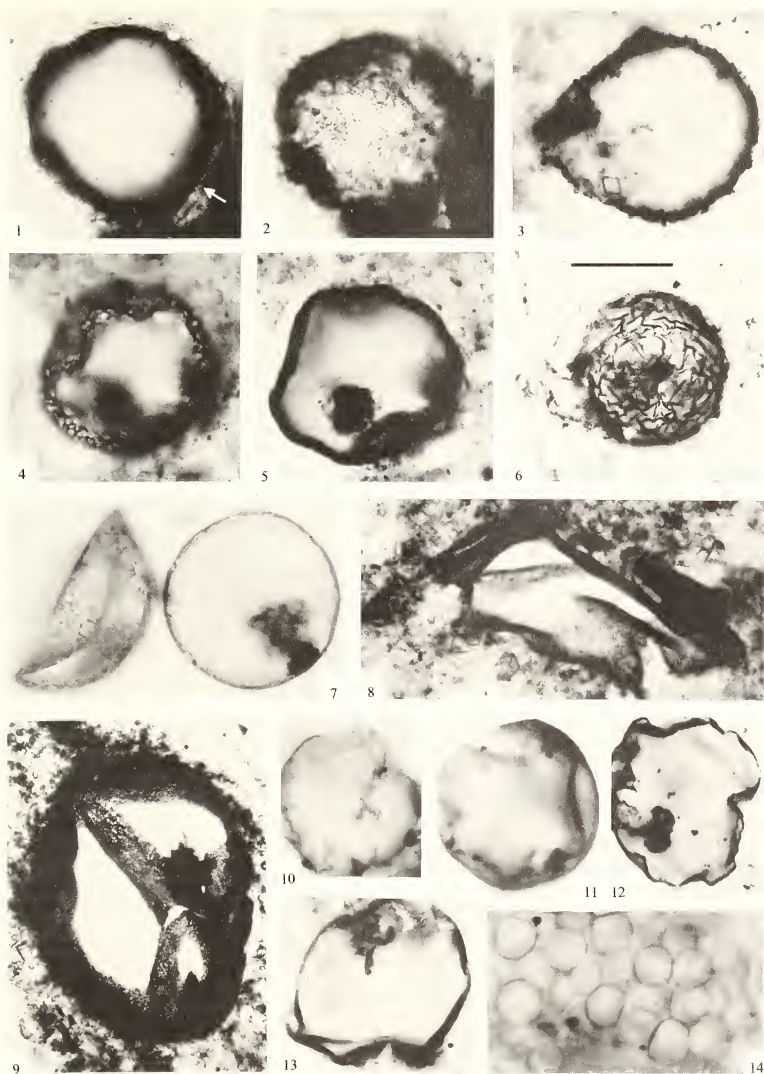
Fig. 10. Cf. *Stictosphaeridium* sp. *sensu* Vidal (1976). K2035-3D, 17.2 $\times$ 122.1, H.U. No. 60656.

Fig. 11. ?*Trachysphaeridium* sp. K1961-3A, 8 $\times$ 124.9, H.U. No. 60661.

Fig. 12. *Kildinella hyperborea* Timofeev. K2035-3F, 3.5 $\times$ 114, H.U. No. 60654.

Fig. 13. *Kildinella sinica* Timofeev. K2035-3K, 5.3 $\times$ 113, H.U. No. 60658.

Fig. 14. *Myxococcoides* sp. K2035-3I, 21 $\times$ 106.4, H.U. No. 60625.



a *Dermocarpa*-like baeocyte producer that was common in glacially influenced environments of the Late Proterozoic era (Moorman 1974; Vidal 1976; Knoll *et al.* 1981). *Palaeopleurocapsa wopfnerii* Knoll *et al.* (1975), described from the Upper Riphean Skilloalee Formation of South Australia, formed filament-like cell arrangements comparable to those found in the modern genus *Pleurocapsa*. Possible *Myxosarcina*-like colonies were illustrated from cherts of the Upper Riphean Boorthanna beds of South Australia by Schopf and Fairchild (1973). Finally, Hofmann (1976) has reported a doubtfully pleurocapsalean colony from the 1900 Ma old Belcher Supergroup, Canada. It is interesting that the three formally described pleurocapsalean microfossil genera—*Bavinella*, *Palaeopleurocapsa*, and *Scissilisphaera*—all compare closely with modern taxa, illustrating both the diversity and the modern nature of the late Precambrian Pleurocapsales.

Class HORMOGONEAE Thuret, 1875

Order OSCILLATORIALES Elenkin, 1949

Family OSCILLATORIACEAE (S. F. Gray) Dumortier ex Kirchner, 1898

Genus EOMYCETOPSIS (Schopf) Knoll and Golubic, 1979

Type species. *Eomycetopsis robusta* (Schopf) Knoll and Golubic, 1979.

Eomycetopsis robusta (Schopf) Knoll and Golubic

Plate 57, figs. 1–4, 8

Description. In the Ryssö Formation, *Eomycetopsis robusta* occurs as a principal mat builder in flat laminated stromatolites, as an associate mat builder with *Siphonophycus kestron*, in oncolites, and as scattered and often fragmented individuals in non-stromatolitic cherts. All Ryssö *E. robusta* sheaths are similar morphologically (cross-sectional diameter range = 2.0–4.0 μm ; $\bar{x}$ = 2.6 μm ; N = 120), but it is not clear that all specimens belong to a single cyanobacterial species. As has been discussed previously (e.g. Knoll 1982a), a number of modern blue-green species belonging to several genera produce sheaths comparable to *Eomycetopsis*.

Genus SIPHONOPHYCUS Schopf, 1968

Type species. *Siphonophycus kestron* Schopf, 1968.

Siphonophycus kestron Schopf, 1968

Plate 58, figs. 4–6

Discussion. *Siphonophycus kestron* was first described from the Upper Riphean Bitter Springs Formation, Australia (Schopf 1968), where populations occur as auxiliary mat builders in association with *Tenuofilum septatum*. *Siphonophycus* sheaths have subsequently been reported from numerous other Proterozoic formations and divided into several species based on size. Members of the Ryssö mat-building *Siphonophycus* populations are slightly larger than those of the original Bitter Springs population (cross-sectional diameter range = 9–18 μm ; $\bar{x}$ = 14.3 μm ; N = 30), but are referred to the type species *S. kestron*. *S. kestron*, like *E. robusta*, is a sheath form species that may have been formed by more than one cyanobacterial species.

Genus TENUOFILUM Schopf, 1968

Type species. *Tenuofilum septatum*, Schopf, 1968.

Tenuofilum septatum Schopf, 1968

Plate 57, fig. 2

Discussion. Specimens of *Tenuofilum septatum* from the Ryssö Formation are indistinguishable from those of the Bitter Springs type population (cross-sectional diameter range = 0.5–1.5 μm ; $\bar{x}$ = 1.0 μm ;

$N = 50$) and like their Australian counterparts, they are interpreted as the sheaths of mat-building cyanobacteria. *Tenuofilum* occurrences in the Bitter Springs and Draken formations are discussed in detail by Knoll (1981, 1982a).

Class HORMOGONEAE Thuret, 1875

ORDER UNKNOWN

Multilamellated Sheath

Plate 57, fig. 6

Description. Filamentous micro-organism, 250 μm long and 39 μm in cross-sectional diameter. Multilaminate construction, with each layer resembling a funnel in which a narrow internal cylinder (20 μm diameter) expands outward to form the filament exterior, the whole resembling a series of stacked funnels.

Discussion. Among previously described microfossils, *Salome svalbardensis* Knoll (1982a), a multi-sheathed oscillatoriian blue-green from the Upper Riphean Draken Conglomerate of Ny Friesland, Spitsbergen, most closely resembles this Ryssö fossil. The Ryssö individual falls within the size range of *S. svalbardensis*, but its lack of a well-defined inner sheath and a preserved cellular trichome precludes more than informal comparison with the Ny Friesland remains. In its general organization, the Ryssö sheath is also comparable to lamellated cylindrical structures from the Skillogalee Formation of Australia illustrated by Schopf (1977). The Skillogalee fossils, informally termed 'Polybessurus' by Schopf, resemble the Ryssö sheath in their 'funnel in funnel' structure, but differ in their much larger diameter (100 μm) and their arrangement as closely packed, vertical tubes in the Skillogalee cherts.

A number of modern filamentous cyanobacteria form divergent multiple sheaths, including members of the genera *Scytonema*, *Petalonema*, *Tolypothrix*, and *Lyngbya* (Golubic 1976a, b; Golubic and Marčenko 1965). Three of these genera belong to the Scytonemataceae, but *Lyngbya* is a member of the Oscillatoriaceae. Thus, while it is likely that the Ryssö multilamellate sheath represents a filamentous blue-green, it is not possible to draw further taxonomic conclusions.

Kingdom PROTISTA

PHYLUM UNKNOWN

Vase-Shaped Microfossils

Plate 61

- 1977 Chitinozoans, Bloeser *et al.*, pp. 676–679, fig. 2.
- 1978 Possibly protozoan microfossils, Fairchild *et al.*, pp. 75–78, pl. 1, figs. 7–9.
- 1979 'Chitinozoan-like' microfossils, Vidal, pp. 24–25, pl. 6.
- 1980 Chitinozoan-like microfossils, Binda and Bokhari, pp. 70–71, fig. 1.
- 1980 Vase-shaped microfossils, Knoll and Vidal, pp. 207–211, fig. 1.
- 1981 Vase-shaped microfossils, Knoll, pp. 46–47, fig. 2.32.

Description. Flask- or vase-shaped vesicles, expanding apically from a rounded base and then tapering gradually toward the apex. Vesicle open at apex; apical opening may appear as a simple truncation of the body or may be bordered by a distinct collar region of varying length. Length = 34–206 μm ($\bar{x} = 106 \mu\text{m}$, $s_x = 38 \mu\text{m}$, $N = 920$); maximum cross-sectional diameter = 16–119 μm ($\bar{y} = 50.5 \mu\text{m}$, $s_y = 16 \mu\text{m}$, $N = 920$); see Table 2. Vesicle walls organic, thick, brittle, psilate when well preserved to pitted when corroded, and rarely collapsed during sediment compaction. Specimens commonly preserved as casts.

Discussion. This taxon is discussed in detail in the body of this paper.

MICRO-ORGANISMS INCERTAE SEDIS

Genus GLENOBOTRYDION, Schopf, 1968

Type species. *Glenobotrydion aenigmati*, Schopf, 1968.

Glenobotrydion aenigmatis, Schopf, 1968

Plate 57, fig. 9

Description. Spheroidal vesicles, 7 to 12 μm diameter ($\bar{x} = 9.2 \mu\text{m}$, $s_x = 1.1 \mu\text{m}$, $N = 70$); walls smooth to finely granular; cells generally contain a small internal body of organic matter. Cells occasionally occur as solitary individuals, but more often occur in irregular aggregates of a few to more than 100 cells. In aggregates, walls often distorted by mutual appression of adjacent cells.

Discussion. The characteristic feature of *Glenobotrydion* cells is the presence of a small, dense, organic granule within the vesicle walls. No matter how one interprets this 'spot'—as coalesced cytoplasm, starch grains, or a partially decomposed organelle—the question of its taxonomic usefulness is open to debate. In the Bitter Springs Formation, *G. aenigmatis* populations are indistinguishable from many of those assigned to *Myxococcoides minor* (small spheroids without internal 'spots') in terms of size frequency distribution, wall structure, patterns of aggregation, or paleoecological distribution (Knoll 1981).

This strongly suggests that many of the specimens segregated as *G. aenigmatis* and *M. minor* belonged to a single biological entity (Hofmann 1976) and that the presence or absence of an internal 'spot' is at least in part a matter of post-mortem cellular degradation. *G. aenigmatis* is here listed as a distinct form species, but it should be borne in mind both that these populations may be closely related to some of the populations assigned to *Myxococcoides* and that several morphologically simple algal species may have converged taphonomically on the *Glenobotrydion* form.

Genus MYXOCOCCOIDES Schopf, 1968

Type species. *Myxococcoides minor* Schopf, 1968.

Myxococcoides spp.

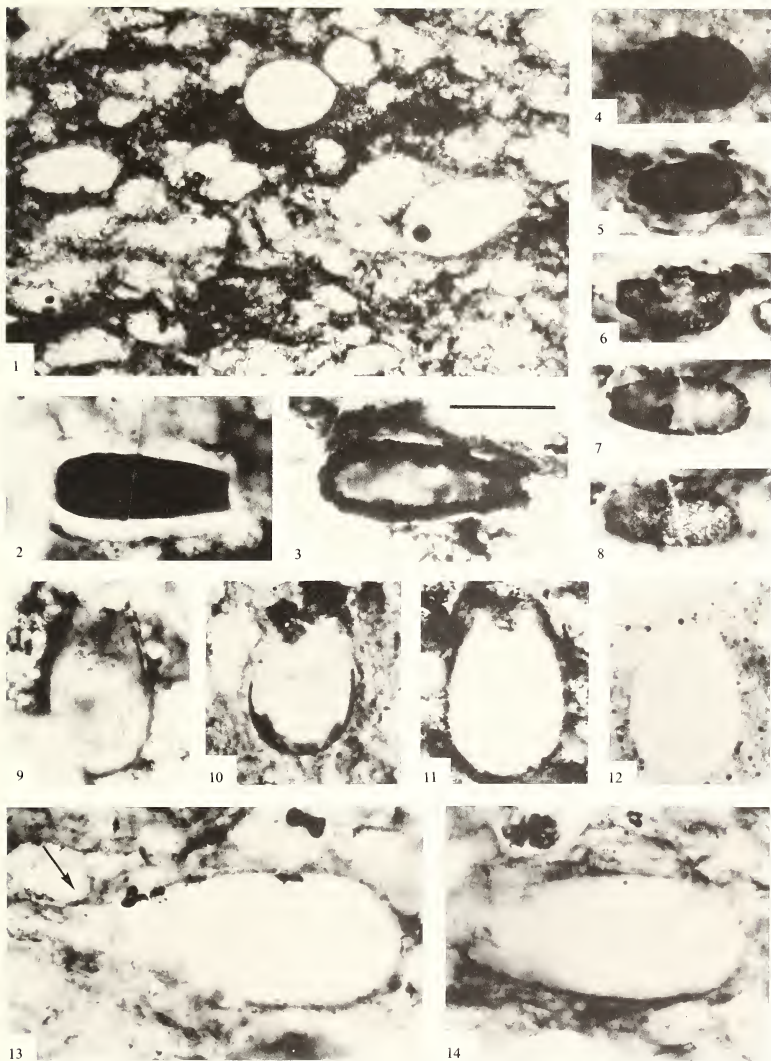
Plate 57, figs. 7, 8, 10; Plate 60, fig. 14

Discussion. Schopf (1968) proposed the genus *Myxococcoides* for the description of certain small spheroidal unicells commonly found in stromatolitic cherts of the Bitter Springs Formation, Australia. The Bitter Springs populations often occurred in colonial aggregates embedded in an amorphous mucilaginous matrix. Species were differentiated on the basis of size frequency distribution, wall characters, and the nature of cell clusters. Over the past decade, the concept of *Myxococcoides* has been enlarged to include a wide variety of small to intermediate size spheroidal vesicles found as solitary individuals or in dense aggregations, and embedded in amorphous organic matter or without extracellular mucilage (Horodyski and Donaldson 1980).

EXPLANATION OF PLATE 61

For each figure, thin section number, stage co-ordinates (where 'x' on slide K2023-1F = 1.9×120.2), and Harvard University Paleobotanical Collection number are given. Bar in Fig. 3 = 100 μm for Fig. 1, and = 70 μm for Figs. 2-14.

Figs. 1-14. Vase-shaped microfossils. 1, low magnification view showing numerous casts in organic rich carbonate, K1929-1A, 23×99.1 . 2, siliceous casts with opaque inner body, K2082-1A, 16.8×116.1 , H.U. No. 60662. 3-8, organic walled specimens. 3, K1924-3A, 5.3×125.8 , H.U. No. 60663. 4, K2082-2A, 6.6×100.2 , H.U. No. 60664. 5, K1929-1A, 9.4×115.5 , H.U. No. 60665. 6, K1929-1A, 18.5×112.1 , H.U. No. 60666. 7, K1929-1A, 17.6×117.9 . 8, same specimen as Fig. 7 in a different focal plane. 9-14, casts in bituminous chert. 9, K2082-1A, 7.5×98.3 , H.U. No. 60667. 10, note partial preservation of organic wall, K1929-1A, 19×104 , H.U. No. 60668. 11, K1929-1A, 22×107.4 , H.U. No. 60660. 12, K2082-2A, 7.5×96 , H.U. No. 60670. 13, arrow points to extended apical collar on cast, K1929-1A, 18.9×99.3 , H.U. No. 60671. 14, K1929-1A, 20.3×101 , H.U. No. 60672.



Microfossils belonging to the genus *Myxococcoides* are common in both the stromatolitic and planktonic assemblages of the Ryssö Formation. Individual colonies fit the diagnoses for a number of previously described species, including *M. minor* Schopf (for Ryssö populations, range = 6–14 μm , $\bar{x}$ = 9.7 μm , N = 140), *M. inornata* Schopf (range = 15–18 μm , $\bar{x}$ = 17 μm , N = 11), *M. cantabrigiensis* Knoll (range = 9–18 μm , $\bar{x}$ = 14.3 μm , N = 185), and *Myxococcoides* sp. C of Knoll, 1983 (scattered individuals in the size range 20–30 μm). Also occurring in these assemblages, however, are numerous solitary individuals which are difficult to place into any single species with certainty, as well as cell clusters and colonies that combine features of several previously described species or 'fall into the cracks' between two species. For this reason, Ryssö myxococcoids are lumped under the designation *Myxococcoides* spp., with the clear understanding that the populations are biologically heterogeneous.

Genus PHANEROSHAEROPS Schopf and Blacic, 1971

Type species. Phaneroshaerops capitans Schopf and Blacic, 1971.

Phaneroshaerops capitans Schopf and Blacic, 1971

Plate 60, fig. 7

Description. Large (30–90 μm), spheroidal vesicle; wall psilate to finely granular, thin, but brittle. Cells occur singly, not in colonies. No apparent extracellular mucilage. Three specimens in the Ryssö Formation have diameters of 43, 46, and 57 μm .

Group ACRITARCHA Evitt, 1963

Genus CHUARIA Walcott, 1899

Type species. Chuaria circularis Walcott, 1899.

Chuaria circularis Walcott, 1899

Plate 60, fig. 9

Discussion. *Chuaria circularis* was originally described from compressed specimens on rock surfaces, and compressions remain the most commonly reported form of preservation for this organism (Ford and Breed 1973; Hofmann 1977). Vidal (1976, 1981a) has extensively discussed macerated *Chuaria* specimens, and his criteria for recognition are applicable to permineralized specimens as well. Like other *Chuaria* populations, the Ryssö fossils are large ($\bar{x}$ = 282 μm , N = 27) spheroidal vesicles with very thick, psilate to chagrinate walls. Most specimens fall in the size range 180–350 μm , although rare specimens up to 800 μm have been observed. A similar size frequency distribution was reported by Vidal (1981a) for several *Chuaria* populations from the Upper Proterozoic Vadsø Group, East Finnmark. The phylogenetic relationships of *C. circularis* are not known; however, its eukaryotic status is indisputable and its relationship to the algae (green algae?) is probable.

Genus KILDINELLA Shepeleva and Timofeev, 1963

Type species. Kildinella hyperboreica Timofeev, 1966.

Kildinella hyperboreica Timofeev, 1966

Plate 60, fig. 12

Discussion. *Kildinella hyperboreica* is a common element in most Late Riphean acritarch assemblages. It is characterized by its robust, psilate walls which are invariably folded in a characteristic fashion. The size range observed for Ryssö specimens is 22–70 μm ($\bar{x}$ = 43 μm ; N = 10). See Vidal (1976, 1981a) for a complete list of *K. hyperboreica* occurrences.

Kildinella sinica Timofeev, 1966

Plate 60, fig. 13

Discussion. *Kildinella sinica* is distinguished from *K. hyperboreica* by its often somewhat granular vesicle surface. Eighteen Ryssö specimens range in diameter from 23 μm to 76 μm ($\bar{x}$ = 40 μm). The two *Kildinella* species occur together in the open coastal Ryssö rocks, as they do in many Upper Riphean formations.

Genus PTEROSPERMOPSIMORPHA Timofeev (1962) 1963

Type species. *Pterospermopsimorpha pileiformis* Timofeev, 1963.

Pterospermopsimorpha sp.

Plate 58, figs. 7, 8

Description. Spheroidal vesicle with two distinct and unconnected walls. Outer wall thick, amber-coloured, well-defined, psilate with numerous fine cracks and wrinkles, 150 to 172 μm in diameter. Inner wall thinner, psilate, 133 to 140 μm in diameter. Large (up to 118 μm), grainy, opaque internal body may be present.

Discussion. Species of *Pterospermopsimorpha* are distinguished by their distinct inner and outer vesicles. Among previously described species, *P. mogilevica* Timofeev (see Vidal 1981a) comes closest in general morphology, although the Ryssö specimens are much larger and contain an additional wall layer. The outer wall of the Ryssö species is virtually identical with acritarchs described herein as Unnamed Form B of Knoll (1983), and it may be that the two fossils are morphological or preservational variants of a single biological species. Unnamed Form B is common in the Ryssö assemblage that contains *Pterospermopsimorpha* sp. Set against this is the fact that in the underlying Hunnberg Formation (Knoll 1983), Unnamed Form B is quite common but *Pterospermopsimorpha* sp. has not been observed.

Genus STICTOSPHAERIDIUM Timofeev (1962) 1963

cf. *Stictosphaeridium* sp. (*sensu* Vidal 1976)

Plate 60, fig. 10

Description. Single walled, spheroidal vesicle 43 to 130 μm in diameter ($\bar{x}$ = 78 μm , s_x = 28 μm , N = 10); walls light and very thin, ornamented by a fine irregular meshwork.

Discussion. Specimens assignable to cf. *Stictosphaeridium* sp. occur commonly in upper Proterozoic clastic rocks. As Vidal (1976) has noted, many of these fossils may be extracellular envelopes that once encased other algae and/or cyanobacterial colonies.

Genus TRACHYHYSTRICHOSPHAERA Timofeev and Hermann, 1976

Type species. *Trachyhystrichosphaera aimika* Hermann, 1976.

Trachyhystrichosphaera vidalii Knoll, 1983

Plate 58, figs. 9, 10

Description. Spheroidal vesicle, double walled; inner wall, robust, finely granular, folded when vesicle is collapsed, 155 to 535 μm in maximum diameter (four Ryssö specimens have diameters of 210 μm , 250 μm , 250 μm , and 255 μm); inner wall bears numerous hollow processes that regularly, but not densely, extend outward from inner wall; processes cylindrical, untapered or tapering gradually toward apex, without internal septations or constrictions, 3 to 8 μm wide and up to 22 μm long; processes support a thinner, psilate to finely granular outer wall or membrane. See Knoll (1983) for a discussion of this distinctive microfossil.

Genus *TRACHYSphaeridium* Timofeev (1966) 1969

Type species. Trachysphaeridium attenuatum Timofeev, 1959.

Trachysphaeridium laufeldi Vidal, 1976

Plate 60, figs. 1, 2

Description. Single walled, spheroidal vesicle, 40–72 μm in diameter (42–50 μm reported by Vidal 1976). A single specimen from the Ryssö Formation is 72 μm in diameter; vesicle surface densely covered by short, conical spines.

Trachysphaeridium levis (Lopukhin) Vidal, 1974

Plate 60, fig. 3

Description. Vidal (1974) described *Trachysphaeridium levis* as a single walled, spherical vesical, 10–100 μm in diameter (polymodal size frequency distribution, with modes in the intervals 30–70 and 80–100 μm); the vesicle was described as 'spongy, having a densely granulate ornamentation'. Two Ryssö specimens having diameters of 56 μm and 92 μm fit this description.

Trachysphaeridium sp. A of Knoll, 1983

Plate 60, figs. 4, 5

Description. Single walled, spheroidal vesicle, 42–65 μm in diameter ($\bar{x}$ = 54 μm , N = 6, compare $\bar{x}$ = 59 μm , N = 16 for a population in the Hunnberg Formation, Svalbard). Vesicle wall robust and well defined, finely granular; wall may retain spheroidal outline or be slightly tuberoso. Specimens occur as solitary individuals.

Trachysphaeridium sp. B of Knoll, 1983

Plate 61, fig. 6

Description. Single walled spheroidal vesicle, 75–210 μm in diameter ($\bar{x}$ = 145 μm , s_x = 63 μm , N = 26; compare to 80–200 μm , $\bar{x}$ = 156 μm , N = 18 for the Hunnberg Formation), with a robust, amber-coloured wall. Wall characteristically psilate, brittle, and finely wrinkled and cracked. Vesicles occur as solitary individuals; no evidence of external mucilage, exocytment structures, or cell division.

Discussion. This common Ryssö fossil is also abundant in the underlying Hunnberg Formation. Its possible taxonomic relationships are discussed by Knoll (1983).

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REVISION OF THE ALATOCONCHIDAE: A REMARKABLE FAMILY OF PERMIAN BIVALVES

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ABSTRACT. Genera and species in the family Alatoconchidae are described and reillustrated, including a major revision of the type genus, and a family concept is established that transfers them from the Megalodontacea to the Ambonychiacea. *Saikraconcha* n. gen., with *S. tunisiensis* n. sp. as type species, and *Dereconcha* n. subgen., with *S. (D.) kamparensis* n. sp. as type species, are described. Two lineages are present in the family, with one including *Shikamaia* and its subgenera *Alatoconcha* and *Tanchintongia*, and the other including *Saikraconcha* and its subgenus *Dereconcha*. Both lineages show similar evolutionary change in form. Alatoconchids are limited in occurrence to the Old World Permian Tethyan province, having a distribution similar to that of the verbeekiniid fusulinaceans. Rapid evolution of species, and their distinctive form, make them stratigraphically useful in the Tethyan province.

Alatoconchids are the most unusual of late Paleozoic bivalves. They are strongly flattened in a dorsal-ventral direction, producing wide wing-like flanges on each valve. Some species had very large and heavy shells, as much as 1 m in length and 10 kg or more in weight, making them nearly the largest known bivalves. Small shells (mostly juveniles) were byssally attached, but large ones were free-living on a soft sediment surface, and are one of the few groups of recliners to have a vertically aligned plane of commissure.

THE alatoconchid bivalves are a distinctive group that differ from other bivalves in their form and large size, and their unusual life habits. These were the Giant Clams of the Permian. The largest individuals in the family probably reached lengths of 100 cm, and had a thick-walled shell up to 3 cm thick. Their most unusual character is the form of the shell, which has wide, alate, wing-like extensions of the valves formed by an isoclinal fold in the shell wall. This produced a very flattened shell, extended in a plane perpendicular to the plane of commissure. They were epifaunal surface dwellers, adapted to a free-living existence on the sea floor, despite large size and great weight. The wide, alate extensions of the shell acted as outriggers to hold the shell up on soft substrate, and to prevent tipping over during rough-water conditions.

Alatoconchids are the largest of all bivalves of the late Palaeozoic, and the most unusual in form, yet they were first described only fifteen years ago. They have been overlooked because of sporadic occurrence, and because they occur in areas where Permian faunas have been little studied. They were strictly tropical in distribution, and were confined to the Old World Permian Tethyan province, having a geographic distribution similar to that of the verbeekiniid fusulinaceans. The unusual form and lack of complete shells in early collections combined to make understanding and description of these bivalves especially difficult. With larger collections available for study, and additional occurrences of alatoconchids documented, it is now possible to resolve questions about characters of the hinge and form that were hurdles to understanding these magnificent bivalves. There are significant differences between species in hinge characters as well as in form, suggesting that there was rapid evolutionary change in the family during the Permian.

PREVIOUS WORK

The family Alatoconchidae and its type genus were introduced concurrently with the description of an unusual late Permian species from Afghanistan (Termier *et al.* 1973). Ozaki (1968) had previously introduced a new genus and species on material from Japan that subsequently could be identified as a member of this family, and Runnegar and Gobbett (1975) also introduced a new genus and species

for material from Malaysia that proved to be related to the Afghanistan material. These three reports were all done on fragmentary material, and when they were written the authors were all unaware of the work done by previous workers. Because of this, no comparisons were made between taxa, and the authors came to conflicting interpretations of the taxonomic relationships and basic form of the shells. Soon after Runnegar and Gobbett completed their manuscript, an investigation of late Permian strata in Tunisia (Newell *et al.* 1976) yielded a collection of specimens clearly related to the Afghan and Malaysian taxa, and a much larger Malaysian collection, with many significant specimens not studied by Runnegar and Gobbett, was assembled from the type locality of their genus.

The limited understanding, and conflicting interpretations, of the taxa made a revision of the group highly desirable. For this purpose most of the Malaysian, Afghan, and Tunisian material has been brought together for comparison. Furthermore, Boyd has studied the Malaysian collection deposited by Runnegar and Gobbett in the Sedgwick Museum at Cambridge, and some of these specimens have been rephotographed. The present paper provides an emended and expanded diagnosis of the family Alatoconchidae, reviews the three previously described genera and subgenera assignable to that family, and introduces one new genus and one new subgenus of alatoconchids.

Considering the fragmental nature of the specimens available to previous workers, and the unusual shell form, it is not surprising that contradictory interpretations of morphology and relationships have been generated by different workers. Ozaki (1968) was unable to assign his material even to phylum, and in reconstruction assumed it to have a form like modern fungoid corals. Termier *et al.* (1973) and Runnegar and Gobbett (1975) were able to determine that their fossils were large, unusual bivalves, but arrived at quite different interpretations about hinge and form and consequently placed them in different orders. This diversity of interpretation obscures the fact that once the basic form is known, the fossils can be seen to be related to each other and to belong in one taxonomic group. The unusual form of these shells has led authors to describe them as 'problematical', 'bizarre', and 'aberrant', and their obscure relationships have given them the status of a mystery group among bivalves.

The report by Runnegar and Gobbett (1975), with its many photographs of specimens and suggested reconstruction of the complete shell, stimulated recognition of alatoconchids by other palaeontologists. Earlier reports were reinterpreted in the light of the Runnegar and Gobbett (1975) reconstruction, and alatoconchids were reported from several new localities. These reports have shown them to occur widely throughout the Permian Tethyan biogeographic province. The remaining task is to determine the character of the hinge and interiors, as well as the true form of the complete shell. Enough material is now available for study to resolve some of these problems, to interpret the taxonomic relationships and life habits, and to explain their biogeographic distribution.

FORM

A major difficulty in understanding alatoconchids is in determining the complete form of a single shell. Shells have several flaring edges which extend in more than one plane, and growing edges were fragile compared to older parts of the shell, so shell breakage was common after death of the animal. The H. S. Lee mine locality in Malaysia has yielded enough material to make possible a complete reconstruction of the shell, and specimens of various growth stages are available for study.

The form of *Shikamaia* (*Tanchintongia*) *perakensis* serves as a model for understanding the fragmentary material of other species, since comparison of available specimens and illustrations shows homology of the major shell features. The alate, wing-like flanges of the shell result from a major extension of the umbonal carinae in both valves, perpendicular to the plane of commissure, so that part of each valve is drawn out into a fold with nearly parallel sides (text-fig. 1). The shell is compressed in the dorsal-ventral direction, and is elongated in the anterior-posterior direction. The ventral surface of both valves is essentially flat, and forms a large planar surface perpendicular to the plane of commissure. Near the hinge the dorsal surface is extended along the plane of commissure to form a dorsal crest extending perpendicular to the flat ventral surface. Thus the anterior portion of



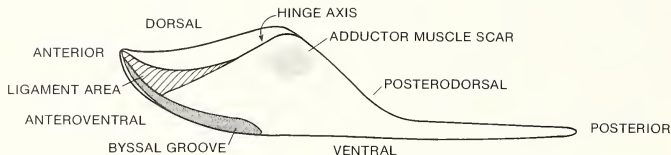
TEXT-FIG. 1. Reconstruction of adult shell form of *Shikamaia* (*Tanchintongia*) *perakensis*, showing dorsal and lateral views. Reconstruction of the posterior end differs from that of Runnegar and Gobbett (1975).

each valve has a triangular cross-section, and the articulated valves have a triangular cross-section on the anterior (beak) half of the shell. The posterior half of the shell consists only of the flat flanges ('wings'), and has a very compressed cross-section. The carinae of the shells have an elliptical outline in dorsal-ventral view, not the roughly parallel outline suggested by Runnegar and Gobbett (1975). A feature present only in juvenile growth stages of *S. (T.) perakensis*, but prominent in several other species, is a collar-like extension of the shell margin around the byssal groove. It projects below the flat ventral surface, opposite the dorsal crest, and is a distinctive feature for this group. All species in the family have significant umbonal infilling, and exhibit considerable allometric change during growth.

A major change in alatoconchid shell form occurs through the Permian as a progressive shortening of the shell along the anterior-posterior axis produced a more rounded outline in younger species, at the same time that compression along the dorsal-ventral axis caused an increase in the proportion of the valve forming the wing-like flange. *S. (T.) perakensis* and *Saikraconcha* (*Dereconcha*) *kamparensis* n. gen. n. sp., the oldest known alatoconchids, have an elongate form and a large body cavity with a high dorsal crest, while *Shikamaia* (*Alatoconcha*) *vainpyra* and *Saikraconcha tunisiensis* n. gen. n. sp., the youngest known alatoconchids, have a nearly rounded outline and more flattened form, which is best developed in *S. tunisiensis*. This form is found in the modern bivalves *Corculum* and *Placuna*, both of which are free-living on the surface of medium- to coarse-grained substrates.

SHELL ORIENTATION

The unusual shell form of alatoconchids makes it difficult to apply the standard conventions of determining anterior-posterior axis on either the hinge axis or the oral-anal axis (Cox 1969), since such orientations would have little relevance to life orientation, and the axis would not correspond with major shell features. Therefore, in this study the anterior-posterior axis is designated as the axis including the beak and abapical end of the shell, and the dorsal-ventral axis is almost at right angles to this, and determined as a perpendicular to the large, flat basal surface (text-fig. 2) This convention



TEXT-FIG. 2. Orientation and location of shell features on right valve of *Shikamaia* (*Tanchintongia*) *perakensis*.

of orientation is doubly convenient, since prominent shell features occur on the axes, making description easy, and it corresponds closely with life orientation of the animal. The ligament-bearing portion of the margin is dorsal, and the byssal groove area (indicating position of foot) is ventral or anteroventral. The large adductor muscle scar, resulting from an anisomyarian musculature, indicates the posterior direction, so the beak end is anterior. This convention is similar to that used for myalinids and mytilids, since all these groups have a produced anterior end and a flattened margin where byssal attachment occurs.

LIFE ORIENTATION

The life orientation of alatoconchids can be inferred from the form of the shell, in combination with its massive character. They are believed to have been epifaunal, with the large flat ventral surface oriented parallel to the sediment surface. This is the only stable position for a very heavy shell, and the ventral surface must have been downward for the byssus and byssal groove to be functional. This position is illustrated (shown in cross-section) by Runnegar and Gobbett (1975) and Thiele and Tichy (1980), but is opposite to that inferred by Termier *et al.* (1973) and Kochansky-Devidé (1978). The latter two reports were on material separated from outcrop and lacking field evidence for positioning, whereas the available field data for *Shikamaia* (*Tanchintongia*) *perakensis* and *S. akasakaensis* show the ventral surface downward to be correct. This should apply to all species in the family.

Modern bivalve genera with a very flattened form provide some useful comparisons. Very flattened form is correlated with free-living, epifaunal habits when the shell is nearly circular in outline—such as the Pectinidae, and the genera *Corculum* (Cardiidae) and *Placuna* (Anomiidae). Alatoconchids like *Saikraconcha tunisiensis* have a form quite similar to *Corculum*, which is flattened in an anterior-posterior direction and has large wings in which the shell is folded in such a way that the sides are nearly parallel to each other. Since the hinges of the two groups are fundamentally different, the similar shapes exemplify convergence in form. *Corculum* lies on the substrate with its wings parallel to the sediment surface. Its nearly flat surface (posterior for it) is up (Bartsch 1947; Kawaguti 1950; Vogel 1975), and it is positioned like a typical cardiid bivalve. In *Corculum*, the anterior projection of the shell houses the foot—an organ of positioning, which on occasion does secrete some byssal threads (Kawaguti 1950)—and the flat posterior surface is adapted for transmitting light to culture endosymbiotic zooxanthellae (Kawaguti 1950; Vogel 1975). From this comparison it is apparent that the flat surface of such a shell indicates horizontality, but does not indicate an up or

down direction for the shell. The location of the foot indicates a down direction, and this can be determined by the position of the byssal opening. Using this relationship, *S. tunisiensis* can be confidently oriented, since it has a byssal notch, indicating the location of the foot. The byssal collar was oriented downward, with the wing-like flanges horizontal on the sediment surface. This is the same orientation as for *Shikania* (*Tanchintongia*) *perakensis*, and supports the idea of ventral-down orientation for all species in the family.

LIFE HABITS

Alatoconchids are inferred to have been epifaunal suspension-feeders, with a reclining habit. The large, wing-like flanges, byssal opening, and very thick, heavy shell indicate an epifaunal habit. Inasmuch as modern epifaunal bivalves are practically all suspension feeders, there is no reason to doubt that this mode of feeding typified the alatoconchids. The heavy, alate, wing-like flanges are functionally adapted for resting on the surface of the substrate, as well as for stabilizing a shell subject to current or wave activity, and are incompatible with an infaunal habit. The byssal opening of smaller specimens indicates either epifaunal attachment or a partially buried endobyssate condition, but the latter condition would be impractical for a shell with wide, wing-like flanges. A very thick, massive shell is associated with epifaunal habit in modern families of bivalves (Ostreidae, Isognomonidae, Chamidae, Tridacnidae), and is very rare among infaunal bivalves. Since large alatoconchids do not have a functional byssal opening, byssal attachment of small growth stages changed to a reclining life habit, lying passive and unattached on the surface of the sediment. Stanley (1970, p. 35) notes that a striking feature of reclining forms is their tendency to develop very thick shells, which is certainly true of the alatoconchids.

Most recliners are inequivalved and pleurothetic (resting on one valve), reflecting their evolution from ancestors cemented by one valve, whereas alatoconchids have a non-pleurothetic orientation, with a vertical plane of commissure. This is a result of evolution from byssally attached ancestors, where the byssus emerged from between the valves. Smaller alatoconchids were byssally attached, and only large alatoconchids achieved a completely reclining life habit. For bivalves with a vertically aligned plane of commissure, a true reclining life habit requires large, flat supporting surfaces on both valves. Even so, the rarity of vertically aligned planes of commissure among recliners suggests that this condition is disadvantageous. Such bivalves have a partly buried shell margin along the supporting surface of the shell, which presents a potential problem with sediment fouling. Whenever the shell opens to allow feeding, the bottom margin opens as well, and sediment could be forced up into the interior of the shell. Being passive animals, the reduced foot was probably of little use in performing a cleaning function when sediment did enter the shell. This functional disadvantage could be alleviated by a minimal shell opening, and by uptilting the abapical shell margins.

The flat basal surface probably did not maintain a truly horizontal position, since the heavy, infilled umbones would tend to settle down into the sediment, at the same time rotating the much lighter posterior end up a short distance above the substrate. This orientation would be beneficial, lifting much of the abapical shell margin a bit above the substrate to improve suspension-feeding capabilities, while reducing the problem of sediment fouling along some of the ventral margin, yet not sacrificing the stability afforded by the wide flanges spread across the sediment surface. A rotation of 10° would have the desired effect, and a consistent down-tipped beak is to be expected of such umbo-heavy shells. This suggests that heavy, infilled umbones are functionally useful in alatoconchids, rather than an accidental feature.

ENVIRONMENTAL SETTING

Alatoconchid occurrences have been referred to as reefs (Salopek 1942, referred to the Yugoslav occurrence as an oyster-bank), and the bivalves have been described as reefal in character (Termier *et al.* 1973). Such interpretations for alatoconchids are not warranted by either their morphology or by their mode of occurrence; none have actually been found in reef deposits, although the Tunisian

specimens are from a stratigraphic interval containing bioherms. The large wing-like flange is poorly adapted for a reef-top environment, but is a good adaptation for life on a loose sediment surface. Furthermore, alatoconchid shells have a regular growth form showing no evidence of crowding during life. While a reef habitat can be ruled out, alatoconchids may have occurred in bank settings (following terminology of Heckel 1974), where large numbers of these large shells created baffles that trapped sediment. However, they appear capable of only limited bank development, and certainly not to the stage of a typical oysterbank. The abundance of alatoconchid shells at localities in Yugoslavia, Malaysia, and Japan suggests that these bivalves tended to live in gregarious clusters. This would explain the large number of specimens found at some localities, in contrast to the relatively small number of localities that have yielded alatoconchids. Both the H. S. Lee locality in Malaysia (see Runnegar and Gobbett 1975, pls. 45 and 46) and a previously unreported occurrence in Japan (K. Ozaki, in correspondence) have many bivalved specimens preserved in life position.

Alatoconchids occur in a matrix of fine-grained sediment containing bioclasts in Tunisia, Afghanistan, Malaysia, and Japan. In the Malaysian and Tunisian occurrences, the rock is light-coloured packstone, poorly sorted, with a bimodal mixture of many broken and complete bioclasts (excluding the alatoconchids themselves) in a fine-grained matrix. Diverse molluscs, and common foraminifers, ostracodes, calcareous algae, and echinoderm plates indicate a shallow depositional environment, probably sublittoral, with moderate or intermittent wave/current energy conditions. The conclusion of Runnegar and Gobbett (1975, p. 321) that *Shikamaia* (*Tanchintongia*) *perakensis* lived in a high-energy environment is not supported by the nature of the sediment, which contains much fine-grained material. In the Afghan and Japanese occurrences, the rock is a dark-coloured, silty, lime mudstone, containing bioclasts and some non-carbonate sediment. The fine grain size and dark coloration indicate low-energy depositional conditions.

The available field information suggests that alatoconchids preferred fine-grained sediment substrates. The large size and great weight of the shell require that the substrate have good bearing strength, such as muddy sand or even stiff mud, but alatoconchids have not been found in winnowed sands or in coarser sediments. They appear to have preferred moderate-energy environments, even if capable of surviving in high-energy environments. Associated fossils—calcareous algae, corals, brachiopods, molluscs—indicate shallow or very shallow water conditions.

GEOGRAPHIC DISTRIBUTION

Alatoconchids occur from the Mediterranean region eastward to Japan. They are known from Djebel Tebaga in central Tunisia (Boyd and Newell 1979), the Velebit Mountains in northern Yugoslavia (Kochansky-Devidé 1978), two localities near Mahallat in central western Iran, and one locality near Shahpoor in the north-western corner of Iran (Thiele and Tichy 1980), two localities (Al-e Say Pass and Bulola Peaks) in central Afghanistan (Termier *et al.* 1973), the Kinta Valley in west Malaysia (Runnegar and Gobbett 1975), and two localities in the Akasaka area in central Japan (Ozaki 1968). This distribution coincides closely with the extent of the Tethyan marine province of the Permian, which occupied the palaeoequatorial zone from the present Mediterranean eastward to east Asia. Alatoconchids are known from all major parts of the province except China, and in future collecting they should be found there as well.

Can the distribution of the alatoconchids be expected to extend to the tropical Permian deposits of the American continents? At present they have not been found in the Americas, and it is reasonable to infer that they will not be found there. The high diversity of organisms, widespread occurrences of reefs, and palaeomagnetic data, all indicate that the Permian strata of west Texas and adjoining New Mexico and Mexico were deposited within a tropical climatic belt, yet no alatoconchids have been found there despite the fact that these sequences are among the most intensively studied Permian deposits in the world. This is not due to absence of the appropriate depositional environment, or to paucity of outcrops. The well-exposed strata contain fine- to coarse-grained siliciclastic and carbonate shelf sediments, and small to large reefs with associated back-reef and basinal fore-reef environments.

Alatoconchids appear to have been excluded from the Americas during the Permian much as modern Indo-Pacific province species are excluded from the Americas today (Emerson 1978).

Since the alatoconchids have a distribution coincident with the Tethyan province as presently known (Yancey 1979), they themselves help define the province, and are an excellent indicator because they are large and easily recognized, even in a fragmentary condition. With this addition, there are three groups of large invertebrates, taxonomically distinct at the family level, which help define the Permian Tethyan province: the bivalve family Alatoconchidae, the fusulinacean family Verbeekiniidae (see Gobbett 1967; Ross 1967), and the coral family Waagenophyllidae (see Minato and Kato 1965; Rowett 1972).

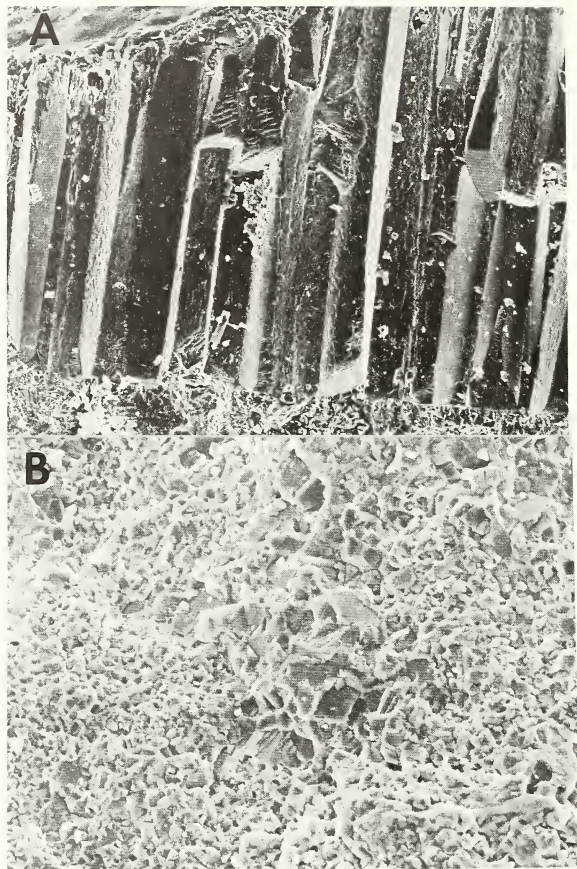
AGE DISTRIBUTION

Alatoconchids are known from an interval including about half of the Permian System. This interval includes the *Pseudofusulina*, *Parafusulina*, and *Neoschwagerina* assemblage zones of the generalized Japanese standard (see Toriyama *et al.* 1974; Minato *et al.* 1978), which corresponds to the Leonardian and Guadalupian series of the Texas succession (see Ross and Nassichuk 1970). No consistent set of stage or zone names has been established for the Tethyan province, so alatoconchid occurrences are referred to in terms of local fusulinid zones where possible. The oldest known alatoconchids, *Shikamaia* (*Tanchintongia*) *perakensis* and *Saikraconcha* (*Dereconcha*) *kamparensis*, are from Malaysian strata of the *Pseudofusulina ambigua* Zone, which Ingavat *et al.* (1980) correlate with the lower part of the Artinskian Stage, and Runnegar and Gobbett (1975) correlate with the lower part of the Leonardian Series. Unidentified alatoconchids of similar age are known from Iran (Thiele and Tichy 1980). *Shikamaia akasakaensis* is reported to occur in the *Parafusulina* Zone of the Akasaka Limestone (Ozaki 1968), suggesting a younger age than the Malaysian or Iranian beds. However, the age determination for the Akasaka alatoconchids is based on fusulinids from loose limestone blocks not directly associated with the bivalves, and possibly derived from other horizons.

The youngest occurrences are from Tunisia, Yugoslavia, and Afghanistan, and are in the *Neoschwagerina craticulifera* Zone and *Neoschwagerina margaritae* Zone and its equivalents, which together make up the *Neoschwagerina* assemblage Zone. In Afghanistan, *Shikamaia* (*Alatoconcha*) *vampyra* occurs in both the *N. schuberti* Zone (= *N. craticulifera* Zone in other areas) and the *N. margaritae* Zone. These two zones are placed in the mid and upper parts of the Murghabian Stage, respectively (Leven 1967). In Yugoslavia, *Saikraconcha ogulincei* occurs in the *N. craticulifera* Zone (Kochansky-Devidé 1978), and in Tunisia, *S. tunisiensis* occurs in strata containing *Neoschwagerina* and *Yabeina*, correlated with the *Neoschwagerina* assemblage Zone (Toriyama 1973, p. 500) and with the Wordian and/or Capitanian stages of the Guadalupian (Newell *et al.*, 1976, p. 83). The concentration of younger Permian occurrences in the western Tethyan province is probably a result of more collecting in this area where younger Permian strata predominate over older Permian strata.

SHELL MICROSTRUCTURE

Alatoconchid shells have an inner shell layer of granular crystals, and an outer shell layer composed of large diameter simple prisms of calcite oriented perpendicular to the shell surface (text-fig. 3). These prisms form a thick (as much as 3 mm) layer over most of the shell, and are much larger than simple prisms occurring in modern bivalves (Taylor and Layman 1972). In *Saikraconcha tunisiensis* the prisms typically have diameters of up to 0.2 mm, and lengths of 3 mm, and in the byssal collar where the outer shell layer is greatly thickened they are nearly 1 cm long. This shell structure is similar to that found in the pinnid and inoceramid bivalves, but differs in the larger size of the prisms. Individual prisms extend across accretion surfaces and traverse the entire thickness of the prismatic shell layer, rather than being interrupted periodically at growth surfaces. Because of their size and coarse texture, these prisms disaggregate easily if the organic sheath around each crystal is destroyed. The sediments containing *S. tunisiensis* contain isolated prisms and bundles of prisms of this sort, much like inoceramid prisms, but larger. The coarse prismatic shell layer of the alatoconchids was



TEXT-FIG. 3. Shell microstructure of *Saikraconcha tunisiensis* n. gen. n. sp. A, coarsely prismatic outer shell layer, outer surface of shell towards top of photograph, and contact with inner shell layer at bottom of photograph, magnification $\times 70$; B, granular inner shell layer, with patches of larger granular crystals (probably due to recrystallization), magnification $\times 200$, from paratype, USNM 353923.

noted in the original descriptions of *Shikamaia akasakaensis*, *Saikraconcha ogulineci*, and *S. tunisiensis*, and has also been observed on *Shikamaia (Tanchintongia) perakensis* and *Saikraconcha (Dereconcha) kamparensis*. The presence of this shell layer could not be established for the available material of *Shikamaia (Alatoconcha) vanipyra*, because of recrystallization.

The inner shell layer of the alatoconchids is composed of a mosaic of granular crystals of calcite. In most cases these are much smaller than the prisms of the outer shell layer, but patches of large granular crystals up to 2–3 mm diameter occur in some shells. The smaller of these crystals may be remnants of original shell material, but it is more likely that in the available specimens the inner shell layers have been completely recrystallized. The lack of correspondence between growth bands (shown by colour) and the areas of large and small granular crystals, together with the crystalline texture, suggest complete recrystallization has occurred. This shell layer was probably deposited as aragonite, which would normally be recrystallized in rocks of Permian age. In *Saikraconcha tunisiensis* there are visible traces of tiny, long crystallites oriented perpendicular to the shell surface, and Kochansky-Devidé (1978) described the microstructure of the inner shell layer of *S. ogulineci* as being finely prismatic.

Shell layers composed of large diameter crystals are very translucent, since there are few crystal boundaries to cause scattering of light. In alatoconchids this is the first shell material secreted by the mantle edge, and thus the growing margins of the shells are highly light-transmissive in a zone a few centimetres wide on either side of the plane of commissure. This may have been utilized to culture symbiotic algal zooxanthellae in the tissue of the animal, an adaptation known to be important in some modern bivalves, and possibly in the extinct rudists (Vogel 1975) and the extinct megalodontids (Fischer 1964, pp. 131–133).

RELATIONSHIPS AND EVOLUTION

The family Alatoconchidae is most closely related to the Myalinidae in the Ambonychiacea, as shown by the duplivincular ligament, thick shell wall, and shell shape. The alatoconchids appear to have had anisomyarian musculature, like their myalinid contemporaries. Runnegar and Gobbett (1975) placed the subgenus *Tanchintongia* in the Myalinidae, but this, and all other genera and subgenera discussed here, differ sufficiently from the myalinids to justify placement in a separate family. The strong, wing-like umbonal carina on juvenile and adult specimens, large shell size, thick coarsely prismatic outer shell layer, and distinct byssal groove warrant recognition of the group as a separate family. In addition, some genera possess a byssal collar, which is unknown in the Myalinidae.

Termier *et al.* (1973) suggested a placement of the Alatoconchidae in the Megalodontacea on the basis of hinge characters. The complex ligament and hinge teeth that they envisioned are now known to be incorrect, and the suggested relationship is invalid. Alate extensions of the hingeline on some juvenile specimens suggest a relationship to the Pteriidae or Bakevelliidae, and the coarsely prismatic outer shell layer suggests possible relationship to the Pinnidae or Inoceramidae, but the possibility of a close relation is precluded by the lack of ligament pits in alatoconchids, the possession of a duplivincular rather than multivincular or mytilid type ligament, and greater similarity of the total form to that of the myalinids. A coarsely prismatic outer shell layer is relatively rare in bivalves, but this feature cannot be taken by itself to indicate a close relationship.

Within the alatoconchids two main lineages can be defined by the character of the hinge. *Saikraconcha* has a simple duplivincular ligament occupying a relatively small ligament area, distinct byssal groove, and large byssal collar, while *Shikamaia* has a modified duplivincular ligament occupying only half of a large cardinal area, has a poorly developed to obsolete byssal groove, and lacks a byssal collar on adults. These differences are found in the Malaysian collection containing *Saikraconcha* and *Shikamaia*, suggesting that the two lineages were established early in the Permian, and persisted into the Late Permian. In both lineages there is a trend from an elongate shell outline for Early Permian species to a rounded shell outline for Late Permian species. Life orientation of the shell does not change during this trend, which culminates in a form and life orientation close to that of the modern genus *Corcum*.

SYSTEMATIC PALAEONTOLOGY

Family ALATOCONCHIDAE Termier, Termier and Lapparent 1973

Diagnosis. Large to very large equivalved shells with elongate or circular outline in dorsal view; shell wall thick, with massive infilling of umbonal cavity, but thin on leading edge; beaks commonly terminal; umbonal carina alate, compressed dorsoventrally and laterally produced, resulting in distinctive wing-like flanges formed by reflexed valve wall; very large flat ventral surface, bounded by umbonal carina; ligament duplivincular; byssal groove present, but non-functional in adults of some species; outer shell layer composed of very large simple prisms set perpendicular to shell surface.

Discussion. It has been called to our attention that the family name Alatoconchidae may not comply with provisions of the International Code of Zoological Nomenclature, Article 11e, which states that 'a family-group name must, when first published, be based on the name then valid for a contained genus', since *Alatoconcha* was inadequately described when first published, and was later placed in synonymy with *Shikamaia*. However, article 40 of the ICZN states that a family group name is not changed, even if a name giver is placed in synonymy, so the family name Alatoconchidae remains valid. The family name was validly proposed at first description, although both the generic and family concepts have greatly changed with subsequent redescription of *Alatoconcha*.

Genus SHIKAMAIA Ozaki 1968

Type species. By original designation, *Shikamaia akasakaensis* Ozaki 1968.

Diagnosis. Very large alatoconchids, lacking byssal collar on adults; with large cardinal area; ligament confined to ventral half of hingeline.

Description. Shells elongated in the anterior-posterior (apical-abapical) direction; beaks terminal; shell roughly triangular in anterior cross-section, and greatly flattened posteriorly; posterior margin pointed, and without gape; ventral surface of joined shells is flat and perpendicular to plane of commissure; beaks slightly upturned away from ventral surface; body cavity small because of massive deposits infilling umbonal cavity and outer edges of flanges; shell wall thick except on posterior margin; hinge lacking teeth; duplivincular ligament located on ventral half of large cardinal area; byssal groove on antero-ventral margin, obsolete on adults; prismatic outer shell layer thin.

Subgenus SHIKAMAIA s.s.

Discussion. Very little published information is available for the type species of the genus. Comparisons with other alatoconchid species have been facilitated, however, by unpublished information obtained from supplementary collections of K. Ozaki (written comm. 1982). The type lot consists of portions of very large shells with posterior shell form similar to that of *S. (T.) perakensis*, except that they are larger and heavier, and have an internal ridge along the dorsal margin of the shell not found in other species. The supplementary material collected by Ozaki reveals the characters of the anterior portion of the shell and shows the full form of the adult shell. *Shikamaia (Shikamaia)* has a very elongate form, and a smaller dorsal crest than other subgenera, is very compressed in a dorsal-ventral direction, and has a small byssal collar during the juvenile growth stage. This subgenus is more closely related to *Tanchintongia* than *Alatoconcha*, but can be distinguished from *Tanchintongia* by its smaller, less massive dorsal crest, presence of a small dorsal niche, and presence of an internal ridge along the dorsal margin of shell. Until the new material came to hand, there was no way to determine the degree of similarity between the two subgenera, but they are now known to be closely related.

Shikamaia akasakaensis Ozaki 1968

1968 *Shikamaia akasakaensis* Ozaki, pp. 28–33, text-figs. 1–5, pl. 7, fig. 1–2; pl. 8, figs. 1–3; pl. 9, figs. 1–2.

Description. Shell with very large wing-like flanges; width across posterior portion of shell as much as 25 cm, and thickness of flange as much as 5 cm; shell outline elongate, with a pointed posterior and anterior ends; length about three times width; dorsal crest small and low; shell wall of wing-like flange averaging 1 cm thick on large specimens; dorsal valve margin thickened internally beside plane of commissure; shell microstructure prismatic in outer shell layer; inner shell layer microstructure unknown.

Discussion. Collection of additional material shows that *S. akasakaensis* is a typical alatoconchid, although larger and heavier than other species. Growth lines on the type specimens show that the shell had a pointed end, and that they are from the posterior portion of the shell. Ozaki (1968) reported that the outer margins of the wing-like flanges are uneven, and undulating, but this appears to represent individual growth irregularities. The distinctive heavy internal thickening along the dorsal valve margin is also found on supplementary material. A few adults of other alatoconchid species show a minor thickening of the valve margin, but the condition is not as pronounced as in *S. akasakaensis*. In common with other alatoconchid species, the dorsal shell wall is thinner than the ventral shell wall, except at the thickened valve margin.

The great width of the type specimens (as much as 30 cm) indicates they reached large size. This is confirmed by specimens seen in outcrop (by K. Ozaki), which have lengths of 60 cm (but incomplete), and width of 20 cm, having a length to width ratio of at least 3 to 1. This indicates that adults reached lengths of 1 m, and possibly more.

This species must be redescribed before detailed comparisons with other species are possible, but it is distinct from all other alatoconchids. Many of the questions about it have been resolved with recently collected specimens, and additional collecting should provide enough material for a detailed description.

Subgenus *TANCHINTONGIA* Runnegar and Gobbett 1975

Type species. By original designation, *Tanchintongia perakensis* Runnegar and Gobbett 1975

Diagnosis. Elongate alatoconchids; wing-like flange and inflated portions of shell forming about equal areas of dorsal surface; pointed beaks projecting far beyond hingeline, and moderately diverging from each other.

Discussion. *S. (T) perakensis* is the best-known alatoconchid species, and is the only one for which early juvenile shell form is known. To the extent that any species or genus in the family can be considered typical, this one is the most representative. It has provided knowledge of the basic form, dorsal crest, wing-like flanges, byssal groove, musculature, hinge, and beak areas, that has made it possible to understand these features on fragmentary or poorly preserved specimens. The recognition of homologous features, such as the byssal groove and wing-like flange, in all species has made it possible to properly characterize the family, and define generic concepts.

Shikamaia (Tanchintongia) perakensis Runnegar and Gobbett 1975

Plate 62

1975 *Tanchintongia perakensis* Runnegar and Gobbett, pp. 316–320, text-figs. 1–2, pl. 45, figs. 1–5 (*non* figs. 6–7); pl. 46, figs. 1–8.

Studied specimens. Nearly thirty specimens in a single lot collected by D. Gobbett and C. T. Tan from the H. S. Lee mine, and housed in the Sedgwick Museum, University of Cambridge, Cambridge, U.K. (SM), and the Department of Geology, University of Malaya, Kuala Lumpur, Malaysia (UM), including the holotype and paratypes, SM G1874, G1875, G1877–1882, and topotypes UM 3070, 3394, 3399, and 4027, and fifteen other unnumbered specimens in the University of Malaya collection.

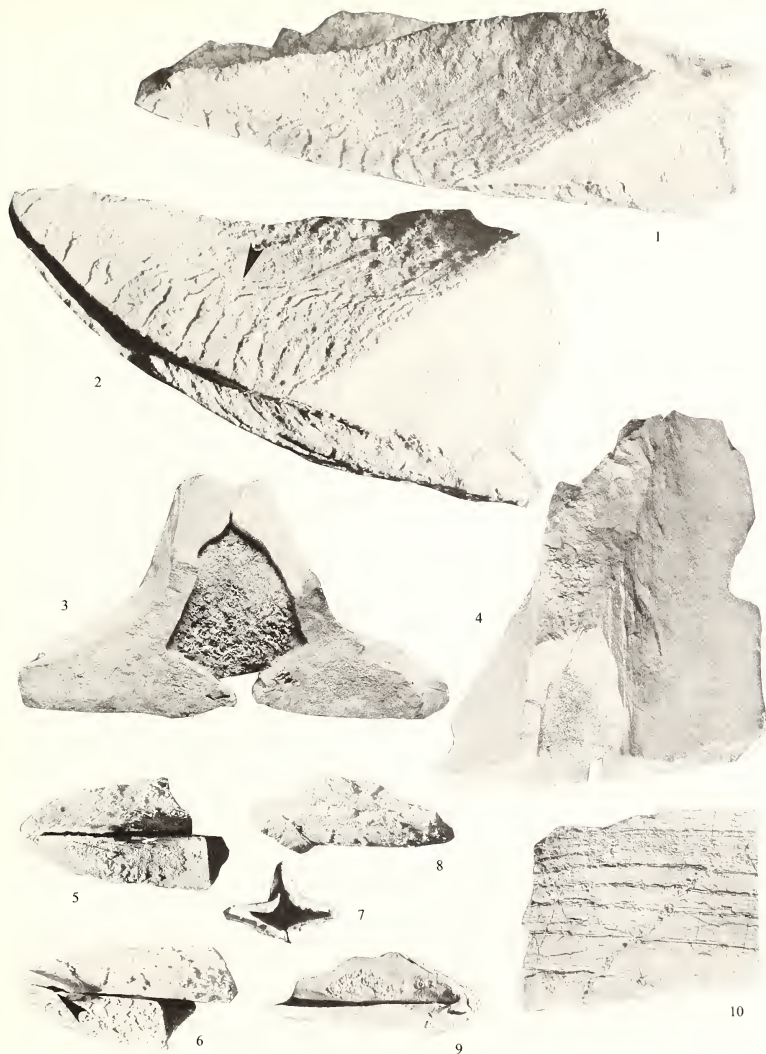
Description: Large equivalved shells; beaks terminal; length several times height or width; triangular transverse section through anterior part of articulated shell (height of triangle is in plane of commissure, and base of triangle coincides with ventral surface); posterior region flattened, resulting in nearly parallel dorsal and ventral surfaces; shell pointed at anterior and posterior ends, and widest and highest in middle (as much as 10 cm height and 20 cm width across both valves); greatest height and width located about one-third shell length from anterior end, with height decreasing abruptly towards posterior, and width tapering gradually towards a pointed posterior end; sharp umbonal carina, expanding posteriorly to form a wing-like flange as much as 10 cm wide; ventral surface of each valve wide, flat, and perpendicular to plane of commissure; umbones infilled with massive deposits as much as 3 cm thick; body cavity small relative to shell size; beaks not appressed; wide cardinal area between beaks and hinge-line; angle between hingeline and ventral surface varies from 15° to 40° , decreasing through ontogeny; hinge lacking teeth; sharply defined duplivincular ligament field covering part of cardinal area; incised ligament grooves aligned subparallel to hingeline except dorsally, where they curve posteriorly, becoming subparallel to dorsal margin of ligament field; narrow byssal groove present on anteroventral margin, directly beneath ligament area; coarsely prismatic shell laminae cross byssal groove at 45° angle, and weather out preferentially, forming a deep groove-like re-entrant on older part of valve; width of byssal groove varies from 3–4 mm on younger shells to 1 cm on large adults; shell wall thickness averaging 1 cm, but as much as 3 cm in apical area, and relatively thin (2 mm) on posterior margin; outer shell layer of coarse prisms, best developed in byssal area.

Discussion. *S. (T.) perakensis* is described from about thirty specimens, including eight specimens of the type lot, and three articulated ones. Runnegar and Gobbett's concept of the form of the shell is modified, especially for the body cavity and posterior regions. Their reconstruction of these regions was based on SM G1880, which is a fragment of the anterior portion of the body cavity, rather than the posterior end. Contrary to their opinion, the shell does not have a noticeable posterior gape, nor a byssal opening in adults. The statement concerning the umbonal septum (1975, p. 316) is based on a specimen assigned here to a different genus. On the other hand, the basic nature of the hinge and the presence of an obsolescent but prominent byssal groove were correctly determined, and the life orientation of the shell and life habits of the adults were clearly indicated. Additional material has greatly increased knowledge of ontogenetic changes in form and life habits.

Hinge. The hinge lacks teeth, and has a short duplivincular ligament. On juvenile shells the ligament extends along the entire hinge-line, but on large shells the ligament extends along only the anteroventral half of the hinge-line. Large shells have a well-defined ligament area on the ventral half of the cardinal area, marked with irregular ligament grooves aligned parallel or at a small angle to the hinge-line. The ventral margin of the ligament area is coincident with the byssal groove, and the dorsal margin is formed by a zone of convergent ligament grooves where the grooves curve sharply towards the body cavity and converge into a narrow zone aligned at a high angle to the hinge-line (see Pl. 62, figs. 1–2). Abapical convergence of ligament grooves to the hinge-line occurs in many

EXPLANATION OF PLATE 62

Figs. 1–10. *Shikamaia (Tanchintongia) perakensis* (Runnegar and Gobbett). 1, 2, UM 3399, dorsal and interior views of beak and apical portion of right valve, showing byssal groove along anteroventral margin, triangular ligament area, with large curved or winding ligament grooves that curve posteriorly at dorsal margin of ligament area (marked by arrow), and apical portion of body cavity. 3, 4, UM 3070, posterior and dorsal views of large articulated specimen, incomplete at both ends. 5–7, UM 4027, dorsal, ventral, and posterior views of articulated juvenile specimen, showing small byssal opening (marked by arrow), and strongly developed wing-like flange on early juvenile part of shell. 8, 9, UM 4027, external and internal views of left valve of juvenile, showing dorsal crest, and growth lines on dorsal and ventral surfaces. 10, UM 3394, ventral view of posterior portion of right valve, with plane of commissure at top of photograph and posterior termination of shell (abapical) to the right. The small angle between growth lines and outer margin of the flange (bottom of photograph) demonstrate a closed, pointed posterior end on the shell (refer to text-fig. 1). All specimens are from the same collection from which the holotype and paratypes were selected. All magnifications $\times 1$ except 3 and 4, which are $\times 0.5$. All from H. S. Lee mine, near Kampar, Kinta Valley, Perak, West Malaysia, H. S. Lee beds, Early Permian.



duplivincular ligaments, but such sharp curvature of ligament grooves has not been observed in other species. Whether this character is restricted to *S. (T.) perakensis* or is a feature of the ligament area of all species of *Shikamaia* is not determinable from the specimens presently available. Another unusual feature of the ligament is its limitation to only half of the hinge-line, in contrast to most duplivincular ligaments which have ligament grooves along the entire hinge-line. This shortened ligament may have arisen as an adjustment to the large size of the adult shell. The irregularity of the ligament grooves on some specimens is unusual, and makes one initially sceptical of their origin as ligament grooves. However, their ligament character is convincingly shown on several specimens because of the sharpness of the incisions, the consistent restriction of the grooves' area to the anteroventral half of the cardinal plate (also noted by Runnegar and Gobbett 1975), and the intersection of the younger grooves with the linear margin of the body cavity.

Byssal notch. Juvenile shells have a deep rounded notch crossing the shell margin very close to the apical end of the body cavity, which forms a circular or heart-shaped opening through the articulated valves as much as 0.5 cm in diameter. It passes through the shell at an angle of about 45° to the anteroventral margin of juvenile shells, and is aligned nearly parallel to the anterior-posterior axis of the shell (see Pl. 62, fig. 9). With growth the byssal opening is extended posteriorly by umbonal infilling, and forms a groove along the anteroventral margin of the valve that is noticeable on all shells, even on strongly eroded ones. In adults a byssal opening is not present (see Pl. 62, fig. 2), but the position formerly occupied by the byssal notch is marked by a zone of easily eroded shell material. The byssal groove is continually being formed as a result of erosion of this weak shell material, which is separated from the body cavity by a thin rim of dense shell material. The weak shell material contains many laminae of coarse, simple prisms set perpendicular to the growth surface, here aligned at 45° to the ventral margin of the shell; these prisms adhere weakly to each other and are susceptible to breakage. Consequently, the byssal groove that is characteristic of *Shikamaia* is secondarily formed, and not from a functional byssal notch. The byssal notch of juvenile shells is proportionally large enough to have contained a byssus capable of anchoring the shell, but the byssal area of an adult shell does not seem large enough to have contained a byssus adequate to support the mass of animal plus shell at this growth stage. The byssal notch was probably closed off by the time the shell reached a length of 10–15 cm.

Size and weight. Reconstructions show that the average length/width ratio for complete adult shells is about 3. Mature articulated individuals with widths of nearly 20 cm are shown in plate 45, figure 8, of Runnegar and Gobbett (1975), and single valves in our collection are almost 10 cm in width. The total length for these shells probably was close to 60 cm, and the dorsal crest extended as much as 10 cm above the ventral surface of the shell. Shell dimensions for typical adults were probably 10 cm height, 20 cm width, and 60 cm length.

The large size and thick shell wall produced a remarkably heavy shell. Many fragmentary valves (free of matrix) weigh over 50 g, and the beak areas alone of smaller specimens weigh up to 300 g. The greatest wall thickness is in the mid-region of the shell around the anterior end of the body cavity. The heaviest shell fragment studied weighed about 1 kg, suggesting about 4 kg for a single valve, and 10 kg total shell weight for an old individual.

Musculature. The animal had a large posterior adductor muscle, and was probably anisomyarian, like myalinids and mytilids. A large (approx. 4 cm²) muscle scar is visible on two shells near the posterodorsal end of the hinge-line. No other muscle scars have been identified, but the observed position of the muscle scar in a shell that is basically mytiliform favours the anisomyarian interpretation.

Subgenus *ALATOCONCHA* Termier, Termier and Lapparent 1973

Type species. By original designation, *Alatoconcha vampyra* Termier, Termier and Lapparent 1973

Diagnosis. Large alatoconchids with wide wing-like lateral flanges extending from anterior to posterior ends of shell; outline of shell margin subcircular rather than elongate; beaks incurved and

nearly touching; dorsal margin of cardinal area on each valve bowed out to enclose a wedge-shaped depression.

Discussion. *Shikamaia* (*Alatoconcha*) differs from other subgenera in characters of form; greater extent of flanges, more rounded outline, having a dorsal niche formed by the curved cardinal areas, and having umbonal cavities. In the original description, it was suggested that the shell had a parivincular ligament, a small secondary ligament, and a large tooth on the hinge. The narrow, arcuate groove interpreted by the authors of *Alatoconcha* as the scar of a parivincular ligament is identical in form and position to the byssal groove of *Tanchintongia*. The features originally interpreted as a secondary ligament pit and tooth appear to be based on imperfections of the fossil. As far as can be determined, the hinges of the two subgenera are the same.

A feature described for *Alatoconcha*, but rare or absent in other subgenera and genera in the family, is compartmentalization within the reflexed part of the valve ('arc-boutant' of Termier *et al.* 1973). Compartments are separated by curved lamellae, concave towards the commissure, which represent periodic withdrawal of the mantle from contact with the shell interior. These probably open to the outside on the posterior end of the shell, and appear to be an accidental rather than normal feature of the shell. They result from trauma to the animal, producing irregular growth, so that shell formation occurred as jumps rather than continuous growth.

Shikamaia (*Alatoconcha*) *vampyra* Termier, Termier and Lapparent 1973

Plate 63, figs. 1-4; text-fig. 4

1973 *Alatoconcha vampyra* Termier, Termier and Lapparent, pp. 75-80, text-figs. 1-6, pls. 13-14.

Type specimens. one large bivalved specimen (holotype) and several smaller fragments (paratypes) all housed in the Palaeontology collections of the Dept. of Earth Sciences, University of Lyon, Villeurbanne Cedex, France. All specimens are unnumbered.

Description. Medium-sized, equivalved shells, reaching lengths of 20 cm, widths of 15 cm, and height of 5 cm; flanges on the anterior portion of the shell are dorsally upturned, producing a curved ventral surface; beaks appressed; wedge-shaped dorsal niche present anterior to dorsal crest, formed by bowed-out cardinal area, and bounded by hinge-line, appressed anteroventral margin of cardinal area, and appressed beaks; hinge-line located on thin shell wall of cardinal platform, which forms wall of umbonal cavity; beaks partly infilled with massive deposits; shell wall thick, as much as 1 cm in beak area; hinge-line aligned at low angle with ventral shell surface; hinge lacking teeth, although a rudimentary bump or node may form at posterior end of body cavity; ligament unknown—probably duplivincular; prominent but narrow byssal groove located along anteroventral margin of cardinal area; byssal groove on large specimens closed off from body cavity by a thin, even rim of shell.

Discussion. *S. (A.) vampyra* is known from one 12 cm long, nearly complete, articulated specimen, and several small fragments of the posterior region of the shell. Termier *et al.* (1973) suggested that *S. (A.) vampyra* is related to the Megalodontidae, because of the strong umbonal carinae, suggested presence of large teeth, and a complex ligament. The feature that Termier *et al.* (1973) interpreted as a tooth is in fact a fragment of the opposite valve, and in that location the valves are not in contact with each other. The feature suggested to be a parivincular ligament groove ('rainure ligamentaire') is the byssal groove characteristic of all species of *Shikamaia*. The feature suggested to be a ligament pit ('fossette ligamentaire') is part of a shallow depression on the anterior end of the body cavity of one valve, and probably varies in prominence from specimen to specimen. Ligament grooves are not discernible on the holotype of *S. (A.) vampyra*, but the arcuate groove on the hinge is a key character in the interpretation of the hinge, and is homologous with the marginal byssal groove of *S. (T.) perakensis*. The dorsal and ventral directions chosen by Termier *et al.* (1973) must be reversed, as must the designation of left and right valves. Their comparison of *S. (A.) vampyra* with the outline of a bat in flight, as shown in the reconstruction drawing (their text-fig. 4) is misleading, and the fanciful name *vampyra* is inappropriate. The irregular form suggested in their text-figs. 1-4 is not characteristic of the shell, which is rather graceful in form. Breakage and deformation have created the irregularities, which were exaggerated in the illustrations.

The apical area and body cavity portions of *S. (A.) vampyra* are similar to those of *S. (T.) perakensis* except for the presence of the dorsal niche and umbonal cavities. The shell wall is as much as 1 cm thick, but is thin on the cardinal platform and the wing-like flanges. The shelf-like cardinal platform is thin on its leading (growing) edge, and makes a rather weak hinge for such a large shell. Shell walls on the flange vary from 1 to 3 mm in thickness, and the flange is about 0.5 cm thick. At the anterior end of the shell, the flange margin extends out nearly perpendicular to the plane of commissure. Growth lines on this part of the shell show that the old position of the plane of commissure has rotated outward 70° – 80° around a pole at the position of the beaks. This suggests a shell with rounded outline rather than one with high length/width ratio.

Genus SAIKRACONCHA new genus

Type species. Saikraconcha tunisiensis new species.

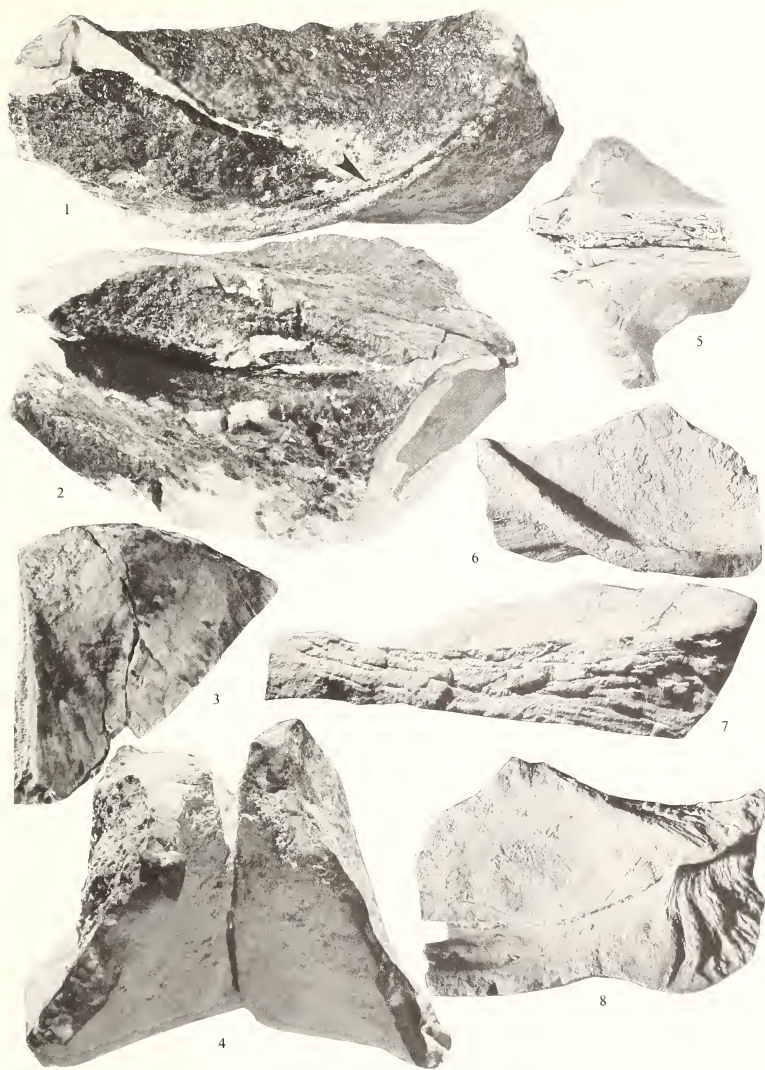
Diagnosis. Alatoconchids with prominent byssal collar on anteroventral margin; byssal groove narrow and deep, and opening into body cavity in adults; ligament area small and extending along entire anterodorsal margin of dorsal crest.

Discussion. The occurrence of an undescribed genus of alatoconchids first became apparent while examining the alatoconchids in the Malaysian collection from Kinta Valley, where two forms are present. The differences were overlooked at first, because very few juveniles of *Shikamaia* (*Tanchintongia*) *perakensis* are available, and there was much uncertainty about the amount of variability to be expected in alatoconchid species. The huge, massive specimens of *S. (T.) perakensis* dominate the collection retained at Cambridge (studied by Boyd), and the remainder of the Kinta collection (studied by Yancey) retained at University of Malaya. The authors of *Tanchintongia* based their description on the large, and common, form, although they included some specimens of the second form as paratypes of *Tanchintongia perakensis*, one of which was illustrated in their publication (Runnegar and Gobbett 1975, pl. 45, figs. 6–7). The two forms have greatly different hinges, and the second form is here placed in a new genus. Two other species of this genus occur in late Permian strata in the Mediterranean area, one in Tunisia and another in Yugoslavia. When first

EXPLANATION OF PLATE 63

Figs. 1–4. *Shikamaia* (*Alatoconcha*) *vampyra* (Termier, Termier and Lapparent), holotype. 1, interior view of anterior part of the left valve, beak to right, with a portion of the dorsal margin of right valve still adhering to it (in upper left corner of photograph), showing byssal groove (marked by arrow) on ventral margin, glycerine-coated. 2, slightly oblique dorsal view of incomplete articulated specimen, showing large wedge-shaped dorsal niche, beaks are broken and wing-like flanges are missing, glycerine-coated. 3, ventral surface of anterior part of left valve, showing lateral extent of flange on anterior portion of shell, beak in upper left corner of photograph, and plane of commissure along left side of photograph, straight margin of lower right side is artificial, and part of a saw cut, glycerine-coated. The portion of the shell to the right of the fracture is not shown in the other figures, but is part of the holotype. 4, anterior view of incomplete articulated specimen, showing arched ventral surface of anterior prow region, and triangular cross-section of valves, beaks are broken and wing-like flanges are missing, coated with ammonium chloride. All magnifications $\times 1$ except 3, which is $\times 0.5$. From Al-e Say Pass, near Dacht-e Nawar, central Afghanistan, *Neoschwagerina margaritae* zone, upper Murghabian, Late Permian.

Figs. 5–8. *Saikraconcha* (*Dereconcha*) *kamparensis* n. gen., n. sp. 5, SM G2695, paratype, anterodorsal view of incomplete articulated shell, showing hinge-line and ligament areas. 6, 8, UM 3380, holotype, external and internal views of nearly complete left valve, magnification $\times 0.8$ and $\times 1.2$ respectively. 7, UM 3380, holotype, enlargement of hinge, showing duplivincular ligament grooves, magnification $\times 2$. All specimens coated with ammonium chloride. From H. S. Lee mine, near Kampar, Kinta Valley, West Malaysia, H. S. Lee beds, Early Permian.



YANCEY and BOYD, *Alatoconchidae*—Permian bivalves



TEXT-FIG. 4. Reconstruction of the shell form of *Shikamaia* (*Alatoconcha*) *vampyra*.

described, these were referred to *Shikamaia* (*Tanchintongia*) on the basis of large size and wing-like flanges. Further preparation of the Tunisian collection revealed a shell like that of the undescribed genus in the Malaysian collection.

During the course of this study the Tunisian specimens were carefully prepared to show the hinge, which differs in part from the interpretations presented by Kochansky-Devidé (1978) and Boyd and Newell (1979). The portion of the byssal collar between the ligament area and the byssal groove was the most baffling feature, and Boyd and Newell (1979, p. 8) noted its resemblance to a resilifer without specifically ascribing such a function to this feature, while Kochansky-Devidé (1978) interpreted the same feature on Yugoslavian specimens as part of the ligament area. This area was carefully prepared on three Tunisian specimens, and the possibility that it is a resilifer or ligament area can be ruled out, on the basis of no ligament grooves, too rough a surface for ligament attachment, and truncated shell layers exposed on this surface. It is a large byssal collar. With the identity of this feature resolved, the hinge is revealed to be of simple form, while the byssal area has complex form.

The two Mediterranean species are the youngest alatoconchids known, and are also the most unusual in form. Several individuals of *Saikraconcha tunisiensis* have almost wavy, or unusually curved, lateral flanges, instead of the nearly flat flanges of most other species of alatoconchids, and they are the most dorsoventrally compressed of the alatoconchids.

Life orientation for species of this genus is interpreted to be the same as for *Shikamaia*. The very flattened form dictates a horizontal orientation for the wing-like flanges, and the functional byssal opening and thickened shell on the same side of the flanges as the byssal collar indicate that the collar was ventral, and the crest was dorsal. This orientation is opposite to that suggested by Kochansky-Devidé (1978) for *Saikraconcha ogulineci* (Kochansky-Devidé), but its similarity to the better-known *S. tunisiensis* provides compelling reasons for reinterpreting the life orientation of *S. ogulineci*.

Derivation of name. From an arbitrary combination of the word Saikra, name of a village and hill in the Djebel Tebaga region, and the term *concha* as used in *Alatoconcha*, the name given for the family name.

Subgenus SAIKRACONCHA S.S.

Saikraconcha tunisiensis, new species

Plate 64, figs. 7–11; text-fig. 3, 5

1979 *Shikamaia ogulineci*, Boyd and Newell, pp. 7–12, text-figs. 8–14.

Type specimens. Twenty-two specimens (most are fragmentary) in a single lot collected by D. Boyd from locality G16 of Newell *et al.* (1976), and housed in the U.S. National Museum, Washington, D.C. Holotype, USNM 258957; Paratypes, USNM 258956, 258958–258962, and 353915–353930.

Diagnosis. Large shells with well-rounded outline, and very flattened along dorsal–ventral axis; umbonal septum on anteroventral margin, between ligament area and byssal notch; large byssal collar; beaks non-terminal, and ventrally down-turned.

Description. Large rounded shells, with width about the same as length; very flattened along dorsal–ventral axis except at anterior end, where a sharp crest occurs on dorsal surface, and a large byssal collar extends below ventral surface; very sharp umbonal carina on anterior end of valves, extending into wing-like flange with limbs 1 cm or less apart; width of flange as much as 15 cm from plane of commissure; flange interior partly infilled in early portions of shell; dorsal crest small, and formed by hinge-line extending away from plane of wing-like



TEXT-FIG. 5. Reconstruction of right valve of *Saikraconcha tunisiensis*.

flanges at a high angle (50° – 70°); ligament duplivincular, with faint, rectilinear ligament grooves, approximately 0.3 mm apart; byssal notch on anteroventral margin, which remained open throughout ontogeny; byssal groove, roughly semicircular in cross-section in each valve, and about 0.5 cm deep in larger valves, extending across middle of wide byssal collar projecting below ventral surface of shell; byssal collar is curved, and with counterpart on opposite valve forms a spout-like opening, bounded apically by appressed beaks; inner surface of byssal collar rough; portion of byssal collar between byssal groove and ligament area covered with curved growth lines, and projects internally along plane of commissure to form a small, thick (as much as 1 cm), blunt umbonal septum; shell wall thick (0.5–2.0 cm) except at distal edges; dorsal shell wall consistently thinner than ventral shell wall; shell wall with an outer shell layer (as much as 2 mm thick) of very coarse (as much as 0.1 mm diameter), simple prisms set perpendicular to shell surface; inner shell layers with a mosaic of granular crystals, probably recrystallized from fine prismatic crystallites.

Discussion. This species is known from a single locality in the Permian strata of southern Tunisia (at the base of unit 16, of measured section G, described in Newell *et al.* 1976, p. 104). As is the case with all other alatoconchid localities, no complete valves are available. The dorsal parts of the valves are lacking in nearly all cases, but the apical region is fairly well determined. The abapical configuration is largely conjectural, but probably is composed exclusively of flat flange; flange margins probably converge abapically without gapping.

The shell is strongly compressed, and umbonal carinae flare widely to form flat, sharp-edged, wing-like flanges perpendicular to the plane of commissure. These give the shell a nearly circular (or heart-shaped) outline in dorsal view. With only small projections perpendicular to the plane of the flanges, the shell approaches *Corculum* in overall form although larger in size. On the anterior end the flange margins meet the plane of commissure at an obtuse angle, producing a V-shaped indentation of the shell margin at the apical end.

The dorsal shell wall of the flange is thinner than the ventral one, and has broken away in nearly all of the collected specimens. This has produced some unusual appearances that have complicated the description and interpretation of this species. On one specimen, breakage of the dorsal shell surface during life of the animal was repaired by withdrawing the mantle from the edge of the flange, and secreting a thinner shell layer between the shell break and the plane of commissure. This is similar to the abrupt withdrawal of mantle edge reported by Termier, *et al.* (1973), but here can be shown to be due to shell damage and injury.

Shell microstructure. Individuals of this species have the best preserved shell microstructure of any species in the family, and in *Saikraconcha tunisiensis* the outer shell layer is quite thick compared to that in other species. The shell has an outer layer (as much as 2 mm thick) of very coarse, simple calcite prisms (as much as 0.1 mm diameter) oriented perpendicular to the shell surface, and an inner shell layer (as much as 2 cm thick). In the outer shell layer each prism crosses growth surfaces and extends across the entire shell layer. Each prism is approximately of equal diameter throughout. They are packed like columns in columnar-jointed rock, and are rather easily separated from each other.

The inner shell layers are recrystallized, but show traces of original microstructure. The present shell fabric is a granular mosaic of fine to coarse crystals, with traces of fine prisms orientated perpendicular to the shell surface, and interrupted by growth lines. The size of these prisms or fibres cannot be determined accurately because of recrystallization, but they are considerably smaller than prisms of the outer layer. They were probably aragonitic and more susceptible to extensive recrystallization than the outer-layer prisms, which were probably originally calcite.

Saikraconcha ogulineci (Kochansky-Devidé, 1978)

1978 *Tanchintongia ogulineci* Kochansky-Devidé, pp. 213–218, text-figs. 1–3.

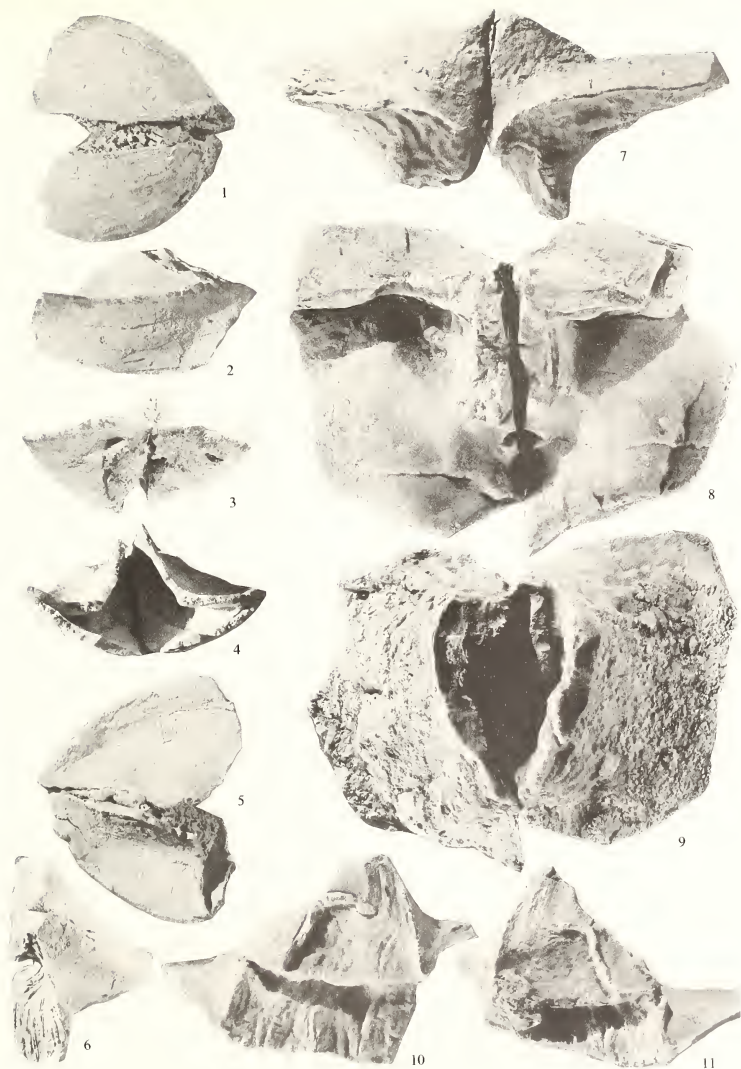
Diagnosis. Large ovoid shells; beaks terminal; umbonal septum present; large byssal collar.

Description. Large shells attaining width of 30 cm; length unknown, but probably greater than width; wing-like flanges relatively narrow, and slightly undulose; umbonal septum present between byssal notch and ligament

EXPLANATION OF PLATE 64

Figs. 1–6. *Saikraconcha (Dereconcha) kamparensis* n. gen., n. sp. 1–5, UM 3372, paratype, ventral (beaks at right), side (exterior of right valve), anterior, posterior, and dorsal (beaks at left) views of articulated, incomplete juvenile specimen, with posterior portion and nearly all of byssal collar missing, showing outline of wing-like flanges and growth lines. 6, SM G1876, paratype, anterior view of left valve, showing prominent byssal groove just below beak (this specimen was illustrated by Runnegar and Gobbett 1975, pl. 45, figs. 6–7). All magnifications $\times 1$. All specimens coated with ammonium chloride. All from H. S. Lee mine, near Kampar, Kinta Valley, West Malaysia, H. S. Lee beds, Early Permian.

Figs. 7–11. *Saikraconcha tunisiensis* n. gen., n. sp. 7–9, USNM 258957, holotype, anterior, dorsal, and ventral views of incomplete articulated young shell, lacking dorsal and posterior regions, dorsal view showing body cavity with distinct byssal opening emerging between valves, anterior view showing downturned beaks, and ventral view showing ovoid opening formed by byssal collars. 10, USNM 258957, holotype, hinge view of anterior portion of incomplete left valve, anterior to right. 11, USNM 258957, holotype, hinge view of right valve, anterior to left, with encrusting coral growing on anterior end of byssal groove and on beak. All magnification $\times 1$. All specimens coated with ammonium chloride. From locality G16 of Newell *et al.* (1976), east end of Djebel Tebaga Range, near Medenine, Tunisia, Saikra biohermal complex, Late Permian.



YANCEY and BOYD, *Alatoconchidae*—Permian bivalves

area; large byssal collar projecting ventrally, with ovoid opening about twice as long as wide; beaks appressed together, and located at anterior end of shell; ligament probably duplivincular.

Discussion. *S. ogulineci* is closely related to *S. tunisiensis*, but differs from it in shell proportions, and placement of the beaks. Kochansky-Devidé (1978) described it as being about twice as long (anterior-posterior) as wide, but this was for a reconstruction, which was probably influenced by the illustrated reconstruction of *Shikamaia* (*Tanchintongia*) *perakensis* published by Runnegar and Gobbett (1975). The semicircular outline of the flanges is closer to the forms of *Saikraconcha tunisiensis* and *Shikamaia* (*Alatoconcha*) *vampyra*, relatively wide shells, than to the wedge-shaped anterior portions of the elongate *S. (T.) perakensis* and *Saikraconcha* (*Dereconcha*) *kamparensis*. The two Mediterranean species of *Saikraconcha* differ most noticeably in the curvature of the beaks. *S. ogulineci* has beaks which touch at the anterior end of the shell. The beaks of *S. tunisiensis* are ventrally downturned, and are not terminal. The two species may attain similar size, reaching widths of about 30 cm, with *S. ogulineci* being more elongate than *S. tunisiensis*. Kochansky-Devidé (1978) estimated a length of 65 cm for *S. ogulineci*, based on the assumption of it being twice as long as wide, but the shell is probably less elongate than shown in her reconstruction.

A slightly undulose character of the flanges was noted in the original description of *ogulineci*: loosely translated 'In side view, the flank edges are somewhat wavy'. This is apparent in both *S. ogulineci* and *S. tunisiensis*, and is puzzling since it seems to be irregular, and without function. The character of the byssal collar and byssal groove are well described by Kochansky-Devidé (1978), but are here reinterpreted. She suggested that the wrinkled growth lines on the interior of the byssal collar were the result of ligament attachment, and inferred a divided ligament area traversed by the byssal groove. This is most unlikely, and by comparison with *S. tunisiensis* it is apparent that the ligament area is confined to the outer edge of what she referred to as a 'keel'. Since this feature projected upward, the term keel is inappropriate, and we refer to it as the crest. Kochansky-Devidé oriented the shell with the beaks upturned, and consequently had the byssal collar upturned. Reversing this orientation brings the byssal area into a more logical location, and better positions other shell features.

DERECONCHA new subgenus

Type species. *Dereconcha kamparensis*. new species

Diagnosis. Shell small and elongate; lacking umbonal septum; having prominent byssal collar, all of which is ventral to byssal groove.

Discussion. This subgenus differs from *Saikraconcha* (*Saikraconcha*) in lacking an umbonal septum. The byssal opening is located at the apical end of the body cavity, adjacent to the ligament area, and the byssal groove runs along the dorsal margin of the byssal collar, rather than across the middle of the collar.

Derivation of name. From an arbitrary combination of the first four letters of the name Derek Gobbett, and the term *concha* as used in *Alatoconcha*, the name-giver for the family name. Through the efforts of Derek Gobbett, formerly of the University of Malaya, and Tan Chin Tong, University of Malaya, a large collection of alatoconchids was assembled during many collecting trips. At present this is the best collection of alatoconchids available.

Saikraconcha (*Dereconcha*) *kamparensis* new species

Plate 63, figs. 5-8; Plate 64, figs. 1-6

1975 *Tanchintongia perakensis* Runnegar and Gobbett, pl. 45, figs. 6-7 (not figs. 1-5 on pl. 45, nor any of pl. 46).

Type specimens. Seven specimens in a single lot of specimens collected by D. Gobbett and C. T. Tan from the H. S. Lee mine, and housed in the Department of Geology, University of Malaya, Kuala Lumpur, Malaysia (UM), and the Sedgwick Museum, University of Cambridge, U.K. (SM). Holotype UM 3380, paratypes

SM G 1876 (this was illustrated by Runnegar and Gobbett 1975), 2695, 2697, UM 3372, and one more unnumbered specimen in the University of Malaya collections.

Diagnosis. same as for subgenus.

Description. Small to medium-sized alatoconchids, elongated in anterior-posterior direction; maximum shell dimensions probably 20 cm long and 10 cm wide; sharp umbonal carinae expand laterally to form narrow wing-like flanges; anterior margin of flange forms 45° angle with plane of commissure; reflexed shell wall of flange forms acute angle in transverse section, rather than parallel-sided fold; hinge-line inclined about 45° to ventral surface, forming large dorsal crest on anterior end of shell; beaks upturned and terminal, producing a prow-like apical end; prominent byssal groove immediately below beak and ligament area, entering shell at anterior end of body cavity; byssal opening rounded, with a heart-shaped cross-section in articulated valves; large byssal collar projecting ventrally below byssal groove, with inner surface formed by irregular, shingled growth layers; ligament area triangular, and located on anterodorsal margin, bounded anteriorly by beak and byssal groove; ligament duplivincular, and consisting of several to many fine, long grooves, almost parallel to hinge-line; shell wall typically 0.5 cm thick, except on growing edges, but as much as 1 cm thick where heavily infilled in beak areas; ventral shell wall thicker than dorsal shell wall; thin outer shell layer of coarsely prismatic calcite, with prisms oriented perpendicular to shell surface; outer prismatic shell layer thickened on byssal collar.

Discussion. This is the smallest of the described alatoconchid species, but clearly reveals its alatoconchid affinities in the wing-like flanges, coarsely prismatic outer shell layer, and its large byssal collar. It is the least specialized alatoconchid, and is probably most closely related to the myalinids, from which the alatoconchids are thought to be derived. The presence of an open byssal notch on the available specimens suggests that it remained attached by byssus throughout life. It is probable that specimens were attached to the very large shells of *Shikamaia* (*Tanchintongia*) *perakensis*, which occur commonly in the same deposit in which *Saikraconcha* (*Dereconcha*) *kamparensis* was collected.

Derivation of name. Named after the town of Kampar, in the Kinta Valley in the state of Perak, Malaysia. Kampar is near the H. S. Lee mine from which the alatoconchids were collected.

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PREDATORY GASTROPODS AND THEIR ACTIVITIES IN THE BLACKDOWN GREENSAND (ALBIAN) OF ENGLAND

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ABSTRACT. The silicified Blackdown Greensand fauna of the Albian in south-west England affords an opportunity for a quantitative assessment of a rich and diverse Cretaceous molluscan fauna. Among its Mesozoic and Neogastropoda are species of naticids and muricids, as well as numerous Opisthobranchia, all of which today are active predators upon invertebrate prey. Drill holes (amongst the earliest yet recorded) into shelled prey provide evidence of their feeding activities. Analysis of the prey preference and drilling behaviour of two of these predator groups indicates that they were essentially similar to those of their living relatives, but predation rates are significantly lower than in either Cenozoic, or Recent faunas.

PERHAPS one of the most notable events affecting marine benthic faunas during the Mesozoic was the appearance and radiation of those groups of animals which today are the major predators in such habitats, in particular teleost fish, crustaceans, and both prosobranch and opisthobranch gastropods (Vermeij 1977). By comparison with their present-day counterparts, we may assume that the activities of these predators had profound effects upon the behaviour and adaptations of prey organisms and upon the structure and organization of benthic communities (Vermeij 1977; Taylor 1981; Hughes 1980a; Bayne 1981).

Gastropods are perhaps the most diverse group of marine predators living today and they experienced a massive evolutionary radiation during the late Cretaceous (Taylor *et al.* 1980), and probably the great range of diets and feeding adaptations associated with this group were largely established at that time. The radiation apparently began in Aptian/Albian times followed by a near exponential increase in diversity, so that by the end of the Cretaceous most of the present-day families can be recognized.

The feeding habits of fossil gastropods can usually only be surmised from a comparison with their living relatives. However, it is well known that three families of prosobranch gastropods contain species which feed by drilling holes into shelled prey; the Naticidae and Muricidae mainly drill into molluscs, whilst the Cassidae bore into echinoids (Carriker and Yochelson 1968; Bromley 1981; Hughes and Hughes 1981). The predatory shell-drilling habit has also been attributed, by various authors at various times, to species in other prosobranch families, namely the Cymatidae, Ficidae, Tonnidae, Nassariidae, and Buccinidae; but as far as we are aware, there are no authenticated observations of shell drilling in these families.

Although holes resembling those made by predatory gastropods are found throughout the fossil record (Bromley 1981 and references) it is generally considered that holes having the morphological characteristics of those drilled by predatory gastropods and occurring in some abundance are not found before the upper Cretaceous (Fischer 1962a; Sohl 1969; Carriker and Yochelson 1968; Dudley and Vermeij 1978; Taylor *et al.* 1980). Although occasional holes which resemble those produced by naticid drilling may be found in pre-Cretaceous fossils, they are usually uncommon and little can be said about them. Therefore, although it is probable that shell drilling by gastropods began before the Albian, we believe that the earliest known fauna in which convincing gastropod drill holes are common, is that of the Blackdown Greensand (Albian) of Devon. The holes are relatively abundant, closely resemble those made by present-day naticids and muricids, and occur in similar positions on the predated shells. Moreover, gastropod species referable to these two drilling families are present in

the fauna. Stanton and Nelson (1980) suggested that the drilling habit was a new mode of predation for naticids at the beginning of the Cainozoic, but it is clear that this habit was established at least fifty to sixty million years earlier.

A growing number of studies have documented the drilling activities of naticid and muricid gastropods during the Cainozoic, examining either their distribution in whole assemblages (Adegoke and Tevesz 1974; Hoffman *et al.* 1974; Robba and Ostinelli 1975), or in individual taxa (Thomas 1976; Dudley and Vermeij 1978; Fischer 1962*b*, 1963; Kitchell *et al.* 1981). However, apart from the data on *Turritella* from the Campanian (Dudley and Vermeij 1978) there are no quantitative data on gastropod drilling predation found in Cretaceous faunas. Therefore we have taken the opportunity to locate the older collections made from the Blackdown Greensand to examine the evidence of drilling and describe the activities of predatory gastropods in the fauna, which on current knowledge seems to be very early in the history of such predation. The gastropods in this fauna show considerable diversity, including many species whose living relatives are carnivores and predators, and consequently in this study we also assess the status, relationships, and relative abundance of such gastropods and consider their possible feeding habits.

The activities of the shell-drilling taxa are documented in terms of prey preference, with some evidence of size selection, feeding behaviour, and the possible effect upon the palaeocommunities. The data from this study may contribute information to support or contradict various hypotheses which have been proposed concerning the development of drilling predation. These hypotheses include:

- (a) Predation intensity has increased from the Mesozoic to the Cainozoic (Vermeij 1977; Dudley and Vermeij 1978).
- (b) There has been a shift in prey preference by drilling gastropods from mainly gastropods in the early Cainozoic to mainly bivalves in the late Cainozoic and Recent (Adegoke and Tevesz 1974).
- (c) Predators may have become increasingly efficient in prey capture and drilling behaviour; for instance, Stanton and Nelson (1980) suggest that even in the Eocene, the wide range of prey and incidence of cannibalism indicate lack of efficiency.

THE BLACKDOWN GREENSAND AND ITS FOSSILS

The Cretaceous outlier of Blackdown Greensand is recognized from published accounts (Downes 1882; Jukes-Browne and Hill 1900) as forming a sequence of more than 30 m of sand and layers of cherty sandstone concretions in North Devon. It is dated as upper Albion on the basis of the many ammonites in the fauna, all of which belong to the *Mortoniceras inflatum* Zone, with the well-established occurrence of the *Orbigny* and *Varicosum* Sub-zones (Hancock 1969, p. 66) and the probability of the *Auritus* Sub-zone at the very top (H. G. Owen, pers. comm.). The majority of the fossils occur in the *Varicosum* Sub-zone.

The deposit, together with the majority of its commoner fossils, was first described by Fitton (1836, p. 236) following his visit there in 1825, but both James Parkinson (1811) and James Sowerby (1813, 1814) had earlier described individual fossils from Blackdown.

Downes (1882, p. 75) described how most early collectors had obtained their specimens from the miners and quarrymen. It was not until he and W. Vicary began to collect *in situ* that any real idea as to the occurrence of the remarkable well-preserved silicified fossils was obtained.

With the closure of the mine workings, it is no longer possible to collect from the exposures in the area. Consequently, our study was completely dependent upon the collections made from the Blackdown Greensand in the last century. Several of the most significant of these collections are in West Country museums, e.g. City Museum, Bristol (Miller collection); Royal Albert Memorial Museum, Exeter (Downes collection); and the Somerset County Museum, Taunton (Fox and Williams collections). Other important material occurs at the Sedgwick Museum, Cambridge (Meyer and Wiltshire collections), at the British Museum (Natural History) (Vicary collection), and the Institute of Geological Sciences, London (Sclater collection).

With the considerable disadvantages of museum collections we have very little information concerning which fossils occurred together. We have had to assume that the relative abundance in collections reflects their natural abundance, although it is very probable that collector bias has resulted in the undersampling of the commoner species and also that thin-shelled, fragile species are also under-represented in collections. Fortunately, Downes's

(1882) thorough examination of the sequence at the eleventh hour, dividing it into twelve beds, has enabled us to gain some idea as to the distribution of the silicified fossils typical of the Blackdown fauna. His description of the beds (pp. 80–4) and lists of the fossils (pp. 85–90) provide the only reliable information that we could use in assessing the co-occurrence of species. In the majority of the beds, the fossils occur in clumps and the two valves of bivalves are nearly always joined; the most fossiliferous beds are found in the centre of the sequence with the shells progressively becoming more worn, separated, broken, and mixed above Bed 8. His observations show that various trigonid species are restricted to certain beds and that the two species of *Glycymeris* do not occur together. *Granocardium proboscideum* is found only in Bed 10; while arcid bivalves are also more frequent in the upper beds. Most specimens of '*Murex*' *calcar* come from the highly fossiliferous Bed 7 and *Turritella granulata* occurs only between Beds 8 and 10. Downes pointedly emphasized that the two species of *Drepanocheilus* co-occur and that the naticid we now recognize as *Forator parkinsoni* is found in Beds 7–10, as are the commoner species of opisthobranchs, whilst *Neithea gibbosa* is characteristic of the uppermost Bed 12.

We have, in addition, a limited number of larger blocks which have survived in museum collections. These have given some idea of faunal association. Most of the molluscs discussed below seem to occur together in the highly fossiliferous Beds 7 and 8.

THE DEPOSITIONAL ENVIRONMENT OF THE BLACKDOWN GREENSAND

The fauna of the Blackdown Greensand, showing an abundance of aporrhaid and turritellid gastropods together with corbulid and venerid bivalves, would by comparison with Recent communities suggest an offshore, sandy bottom fauna living at water depths of between 15 and 85 metres.

The limited evidence we have indicates that we are discussing several assemblages with many taxa in common. These are what is preserved of fluctuations in faunal composition apparently dependent upon slight variations of the sediment.

Communities dominated by turritellid gastropods are known throughout the world from water depths of approximately 15–50 m (Thorson 1957; Buchanan 1957; Dörjes 1971; Wu and Richards 1981; Powell 1937). Aporrhaid gastropods today have a fairly restricted geographical distribution, but are found abundantly with *Turritella* in the Irish Sea (Jones 1956), off the Atlantic Coast of Spain (Cadée 1968), the Mediterranean (Thorson 1957), and off the eastern coast of the U.S.A. (Perron 1978). Such *Aporrhais* and *Turritella* dominated communities often grade laterally into the so-called '*Venus*' communities which contain abundant venerid bivalves, *Corbula*, *Spisula*, *Tellina*, and naticid gastropods (Thorson 1957).

The 'oceanic zone' community developed on sand at 40–85 m off the Atlantic coast of Spain (Cadée 1968) has abundant *Turritella* and *Aporrhais* together with *Natica*, several predatory neogastropods, as well as abundant *Glycymeris*, species of *Cardiidae*, *Veneridae*, *Tellinidae*, and *Corbula*. This fauna seems to be very similar in character to that of the Blackdown Greensand. Trigonid bivalves are, of course, absent from these modern communities, but species of their probable ecological equivalents, the *Cardiidae*, are frequently abundant.

THE GASTROPODS AND THEIR TROPHIC POSITION

The Blackdown Greensand gastropod fauna comprises at least sixty-five species, including fifty-seven prosobranchs and eight opisthobranchs (Table 1 and Appendix 2). It was considered necessary to provide systematic descriptions for the predators referred to in this study and the authors have published their revised nomenclature elsewhere (Morris and Cleveley, in press). Authorities for species may be found in the Appendix.

The most abundant gastropod family is the Aporrhaidae, which comprise 34% of the total gastropod numbers (text-fig. 1). Nine species have been recorded but only three of these, namely: *Perissoptera parkinsoni* (83 individuals); *Drepanocheilus neglecta* (275); and *D. calcarata* (956), are common. A similar abundance and diversity of aporrhoids occurs in other marine Albian deposits of north-west Europe. Both *D. neglecta* and *D. calcarata* appear to be endemic to the Blackdown facies although closely similar species are found elsewhere. Living aporrhoids feed upon epilithic algae, diatoms, and detritus (Perron 1978).

The Turritellidae, particularly *Turritella granulata* are the next most abundant gastropod group, comprising 18% of individuals. Living *Turritella* are shallow-burrowing ciliary suspension feeders (Fretter and Graham 1962). Other herbivorous groups represented are the Trochacea, Cerithiacea, Rissoacea, and Littorinacea (Fretter and Graham 1962; Houbbrick 1974, 1978).

TABLE 1

a. Ranked abundance of gastropods in the Blackdown Greensand fauna by family or superfamily

	Individuals	Species
1. Aporrhaidae	1,325	9
2. Turritellidae	706	2
3. Acteonidae	497	4
4. ' <i>Murex</i> ' <i>calcar</i>	380	1
5. Naticacea	302	4
6. Cerithiacea	174	13
7. Muricacea (<i>sensu</i> Ponder 1973)	145	12
8. Littorinacea	124	1
9. Ringiculidae	79	1
10. Trochacea	75	4
11. Epitoniidae	35	3
12. Pyramidellidae	24	2
13. Rissoacea	13	4
14. Fossaridae	9	2
15. Vanikoridae	3	1
16. Scaphandridae	2	1
17. Pleurotomariacea	1	1
	3,894	65

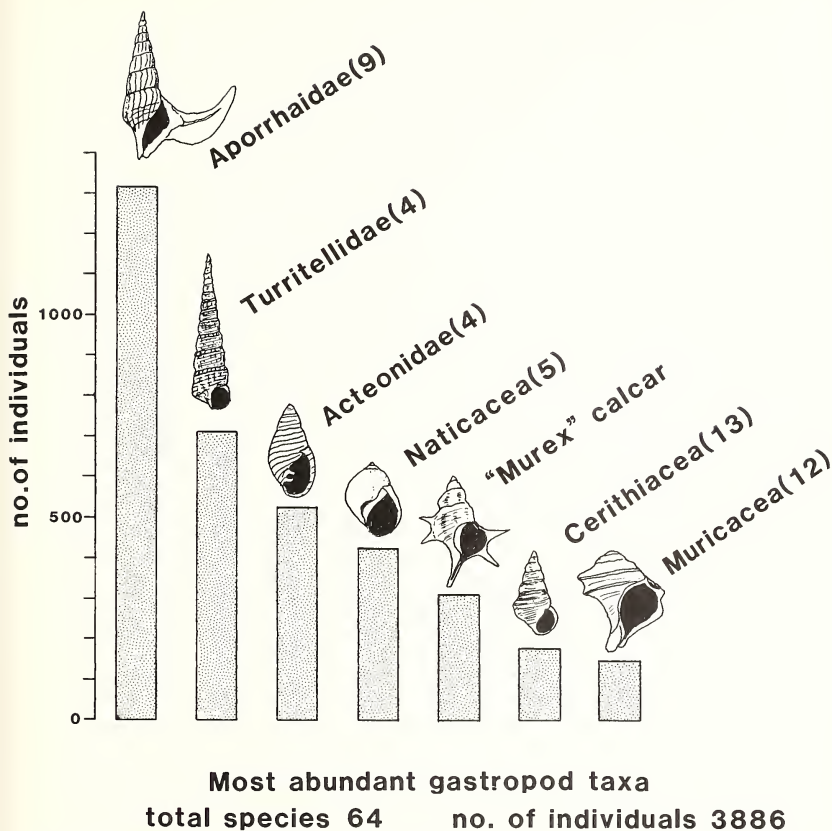
b. Ranked abundance of the most common gastropod species

1. <i>Drepanocheilus calcarata</i>	956
2. <i>Turritella granulata</i>	704
3. ' <i>Murex</i> ' <i>calcar</i>	380
4. <i>Tornatellaea affinis</i>	356
5. <i>Drepanocheilus neglecta</i>	275
6. <i>Forator parkinsoni</i>	189
7. ' <i>Littorina</i> ' <i>conica</i>	124
8. <i>Cirsocerithium gracile</i>	122

We are uncertain of the systematic position of another of the more common gastropods, '*Murex*' *calcar*. Although it possesses some morphological features in common with the Miocene to Recent genus *Murex sensu stricto*, we believe that these result from convergence. For the present paper, our conclusion is to consider '*M. calcar*' as belonging to an undescribed genus of the Mesogastropoda, that is perhaps related to the Strombacea.

There are three species of Epitoniidae in the fauna; all living members of this family are carnivorous, feeding upon various soft-bodied or skeletalized anthozoans (Robertson 1970, 1980).

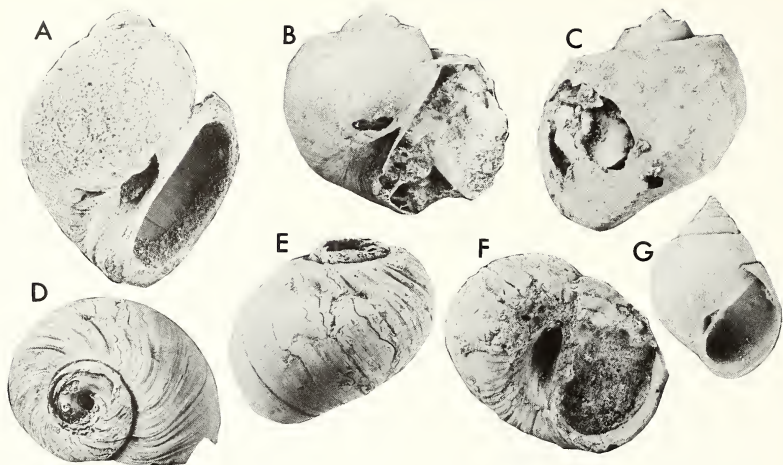
Four species, comprising 302 individuals, can be referred to the Naticacea (text-fig. 2); in order of abundance these are: *Forator parkinsoni* (63%); *Pictavia rotundata* (25%); *Gyrodontia gentii* (9%); and *G. dupinii* (3%). Living naticaceans are active predators feeding by shell drilling, largely upon molluscan prey (Ziegelmeier 1954; Edwards 1974). Naticacean gastropods are known from the lower Jurassic, but drill holes that can confidently be attributed to their activities are not recognized in any abundance before the Albian (Sohl 1969). The inevitable conclusion is that pre-Albian Naticacea were not shell drillers. Three of the Blackdown naticids, *G. gentii*, *G. dupinii*, and *P. rotundata*, occur in other Albian and Aptian deposits, in which drill holes have not been found. *F. parkinsoni*, the most abundant naticid in the fauna, appears to be restricted to the Blackdown Greensand apart from a few small specimens in the Gault. This species is quite distinct in shell morphology from any earlier naticid taxa, and is the probable drilling predator amongst the Blackdown naticids. The other naticids are assumed to be carnivores and possibly, like some living naticids, they fed upon bivalves without the necessity



TEXT-FIG. 1. Relative abundance of the seven most common gastropod taxa in the Blackdown Greensand samples.

of drilling (Turner 1955; Vermeij 1980). Most pre-Albian naticids have been classified in the subfamily Ampullospirinae and Sohl (1969) considered that the first naticid drill holes coincide with the first appearance of members of the subfamily Polinicinae during the Albian. However, the assignment of Mesozoic naticids to one or other of the Recent families is a highly subjective exercise.

Twelve species of gastropods comprising only 4% of the total individuals may be referred to the order Neogastropoda. Most living taxa in this order are active carnivores and predators (Taylor *et al.* 1980); exceptions are a few species of Nassariidae and Columbellidae which are detritivores and herbivores. Although we are confident that these twelve are neogastropods, it is difficult solely on the basis of shell characters to refer



TEXT-FIG. 2. Naticacea from the Blackdown Greensand. A, *Forator parkinsoni* Morris and Cleavelly, BM(NH) 57302, $\times 2$. B, C, *Gyrodes gentii* (J. Sowerby), BM(NH) 34755, both approx. $\times 2$. D, E, F, *Gyrodes dupinii* Deshayes and Leymerie, BM(NH) G 16112, $\times 3$. G, *Pictavia rotundata* (J. Sowerby), BM(NH) G 16154, Vicary Colln., $\times 3$.

them to higher taxa. Ponder (1973) provided the most recent review of relationships within the order and all of the Blackdown species apparently fall into his superfamily Muricacea; there are no examples of the Conacea and probably none of the Cancellariacea. The Muricacea (*sensu* Ponder) is a large taxon comprising most neogastropod families, but the relationships of the component families are at present obscure.

Amongst the twelve species (text-fig. 3) of neogastropods that we have recognized, five (comprising 54% of individuals) have shell characters that compare well with certain Muricidae, particularly those that have a less specialized shell form than either the Muricinae, or the Typhinae which we have not recognized before the Maastrichtian.

?*Paramorea lineata* is a small whelk-shaped species quite distinct from others in the fauna, it differs from *P. lirata* Wade (Campanian, U.S.A.) in lacking a ramp to the whorl and having a less truncated siphonal fasciole. Wenz (1938) placed the *Morea* group of genera in the Drupinae (= Thaidinae) and Stephenson (1941) introduced a family Moreidae (now Moreinae). *Morea* and *Paramorea* are similar in general shell form to species of present-day Thaidinae and although we have as yet no succession of these taxa through the Cretaceous-Tertiary boundary, we suspect that the Moreinae are early Thaidinae. The vast majority of living members of this family feed by drilling sedentary prey, e.g. other molluscs and barnacles, although a few species eat polychaetes, sipunculids, or corals (Taylor 1976, 1978).

Four other species occurring at Blackdown are somewhat similar to the living genus *Rapana*, considered to have a primitive shell form for the Muricidae, in having large equi-dimensional apertures and short upturned necks. *Semipirum depressum* has a large tangential aperture with virtually a flat spire that has a tendency towards a limpet-like form. There is a suggestive similarity to the Recent alcyonarian-feeding genus *Rapa*, but the limpet-like shape may be due to convergence, as occurs in the thaid limpet *Concholepas*. It is suspected that this shape is probably an adaptation for clinging to hard substrate. The similarity of ornament and whole shape to *Hillites downesi* and *Culmia brighti* are thought to be of more taxonomic significance and suggest that *S. depressum* may be a limpet-like early rapanid.

H. downesi has a distinct spire, a sharply incurved neck, and a relatively smaller tangential aperture. We agree

with Stephenson (1952, p. 181) that this genus may be related to *Sargana*, but find some difficulty in deciding whether the Sarganinae should be synonymized with the Rapaninae. *Sargana* has a more advanced aperture and delimited anterior canal than occurs in living *Rapana*, characters that resemble those of living Coralliophilidae. Although particularly concerned at the lack of *Rapana*-like taxa in the upper Cretaceous, we have tentatively included *Hillites* in the Rapanidae.

C. brighti has the generalized shell form of *Rapana* but with only fine spiral ornament. It is similar to *Ecphora* (?Cenoman.-Plio.) which suggests inclusion of *Culmia* in the Rapaninae.

Blackdownia quadrata has different shell ornament and apertural shape to *C. brighti*, and is a taller species. Although we follow Kollmann (1976, p. 196) and include this species in the Rapaninae, its form but not its ornament resembles *Forreri*, better placed in the Trophoninae, rather than *Rapana*. Shell shape also indicates some similarity to species of the genus *Pyropsis* (Cretaceous, see Sohl 1964, pl. 34) which have been placed in the Vasidae. Comparable intermediate vasids, with long and short siphonal canals, are still living (Abbott 1959), but their biology is not well known. Although Sohl may be correct in his assignment of *Pyropsis*, we consider that *Blackdownia* has a much more upwardly twisted shell neck than is found in that genus. Present-day Rapaninae feed by drilling both epifaunal and infaunal bivalves and live upon both sandy and rocky substrates (Gomoiu 1972).

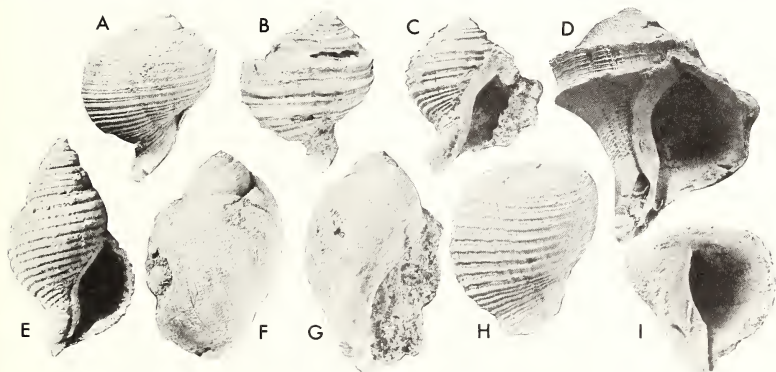
Four of the Blackdown species can be confidently assigned to the family Fascioliariidae as currently recognized but which we consider to be paraphyletic.

Resabulum rusticum is a squat, rather whelk-shaped fascioliariid that closely resembles a number of north-west European Palaeocene species that have been wrongly attributed to *Siphonalia*, particularly '*Siphonalia*' *mariae* (Melleville) from the Thanet Sands, a similar facies to the Blackdown Greensand.

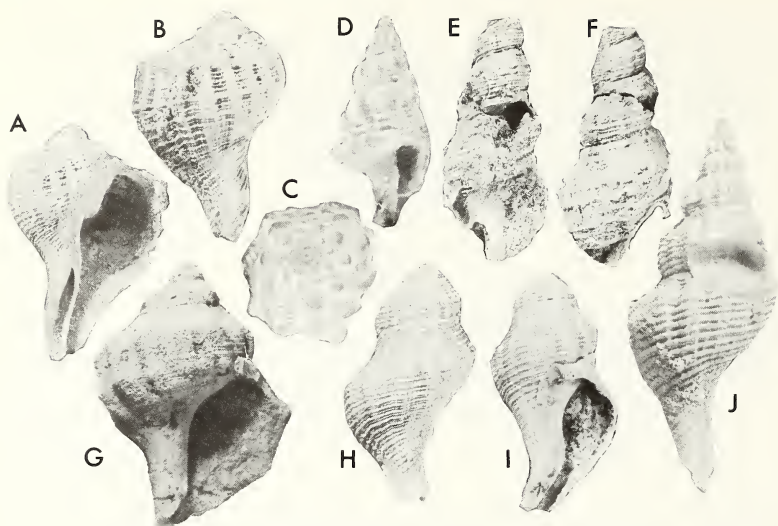
Iscafus *rigidus* is one of the commoner species of neogastropods occurring in the Blackdown Greensand and is also relatively frequent in the Gault Clay facies at Folkestone. It is much taller than *R. rusticum* and has a form superficially similar to *Pleuroploca*, or *Palaeosephia*.

Dummonia collisnigrae has a last whorl that is closely comparable to that of *I. rigidus*, but its earlier whorls are much more depressed and rounded. Finally, a fragment of '*Fusus*' *dubius* shows the tall turreted spire typical of the Fusininae.

Living species of Fascioliariidae feed upon polychaetes and molluscs; it is the larger forms such as *Pleuroploca* that feed upon molluscs (Paine 1966 and J. D. Taylor, pers. observation) whilst the smaller forms such as



TEXT-FIG. 3a. Muricacea and possible Muricacea from the Blackdown Greensand. A, *Hillites downesi* Morris and Cleveley, Exeter Museum, Downes Colln., $\times 4$. B, C, *Culmia brighti* (J. de C. Sowerby), Exeter Museum 97/1971, Downes Colln., $\times 2$, from upper Greensand, Coombe Raleigh, nr. Honiton, Devon. D, *Blackdownia quadrata* (J. de C. Sowerby), BM(NH) G 16153, $\times 1.5$. E, ?*Paramorea lineata* (J. de C. Sowerby), BM(NH) GG 20975, $\times 5$. F, G, *Cosmia cosnensis* (de Loriol), Taunton Museum 7304, Fox Colln., $\times 3$. H, I, *Sempirum depressum* (J. de C. Sowerby), H, IGS 6851, $\times 3$, I, Sedgwick Museum B 44819, $\times 3$.



TEXT-FIG. 3b. Fascioliariidae, ?Melongeniidae, and ?Mitridae from the Blackdown Greensand. A, B, *Tantunia clathrata* (J. de C. Sowerby), BM(NH) 34838, A, $\times 3.5$, B, $\times 3$. C, D, ?Mitridae, BM(NH) GG 21286, Vicary Colln, C, $\times 10$, apical view, D, $\times 8$ (note the four plaits on the columella). E, F, ?Fascioliariidae, IGS 5763, $\times 2.5$. G, *Resabulum rusticum* (J. de C. Sowerby), Bristol Museum Ca 5637, $\times 2$. H, I, *Dumnonia collisnigrae* Morris and Cleveley, Taunton Museum 7502, $\times 2.5$. J, *Iscafusius rigidus* (J. de C. Sowerby), Sedgwick Museum B 44899, $\times 3$.

Fusinus, *Peristernia*, *Cantharus*, and *Leucozonia* mainly eat polychaetes, although they occasionally eat small gastropods (Taylor 1978 and unpublished records). As the Blackdown fascioliariids are all small they would be expected to have been polychaete feeders.

Each of the remaining three species have characters in common with different neogastropod families. One unnamed species (text-fig. 3) has a fascioliariid shell form, but three prominent columellar plaits suggest that it could have been an early mitrid. The mitrids may have been an early offshoot of the fascioliariid paraphyletic stem group. Most living Mitridae that have been studied feed upon sipunculid worms (Taylor *et al.* 1980).

Cosnia cosnensis has no columellar plaits but in other ways resembles the upper Cretaceous genera *Ptychoris*, *Ficulomorpha*, and *Palaeatractus*, all traditionally placed in the Volutidae, and *Malaxa* which Sohl (1964, p. 267) referred to the Cancellariidae. The Cenomanian genus *Carota* Stephenson (1952, p. 184) appears to be the earliest with the characteristics of the Volutidae and is quite different from this group of genera. Further, we remain unconvinced that they belong to the Cancellariacea. Consequently, we are uncertain as to their correct position. Present-day Volutidae mainly feed upon other Mollusca (Taylor *et al.* 1980).

Tantunia clathrata bears a superficial resemblance to the *Busycon* group, normally placed in the Melongeniidae. If these similarities do not indicate a close relationship, they may at least indicate a comparable mode of life. Most living members of the Melongeniidae feed upon other molluscs (Paine 1963; Hathaway and Woodburn 1961).

Shelled opisthobranchs are diverse and abundant in the Blackdown fauna, comprising 16% of the total gastropods (text-fig. 4). Four species can be referred to the family Acetonidae; one, *Avellana incrassata*, to the Ringiculidae; and one, *Cylichna*, to the Scaphandridae. The Acteonidae, with the two commonest species



TEXT-FIG. 4. Opisthobranchs from the Blackdown Greensand. A, *Tornatellaea ebrayi* de Loriol, BM(NH) GG 20980, Vicary Colln, $\times 4$. B, *Tornatellaea affinis* (J. de C. Sowerby), BM(NH) GG 20986, Vicary Colln, $\times 4$. C, ?*Lacrimiformia pusilla* (J. de C. Sowerby), BM(NH) G 16110, Vicary Colln, $\times 4$. D, *Tornatellaea* cf. *unisulcata* de Loriol, BM(NH) GG 20990, Vicary Colln, $\times 5$. E, *Tornatellaea* cf. *cosnensis* de Loriol, BM(NH) GG 20989, Vicary Colln, $\times 5$. F, *Avellana incrassata* (J. de C. Sowerby), BM(NH) G 704, Sir P. de Malpas Grey Egerton Colln, $\times 5$. G, *Cylichna* sp. cf. *urgonensis* Pictet and Campiche, Sedgwick Museum, Cambridge B 45015, $\times 10$.

Tornatellaea affinis and *T. ebrayi*, form the largest single group of predatory gastropods in the Blackdown fauna. All living species of acteonid gastropods that have been studied feed upon polychaetes (Hurst 1965; Rudman 1972; Taylor, in prep.). The data are much less satisfactory for *Ringicula*, but a few gut samples (Pelseneer 1925; Fretter 1960) have recorded foraminifera and interstitial copepods. Study of various species of Scaphandridae, including *Cylichna*, indicates that they feed upon small bivalves, gastropods, foraminifera, and echinoderms (Thompson 1976).

Two species may be referred to the genus *Lacrimiformia* which Sohl (1964) has assigned to the Pyramidellidae. Many living species of this family are parasitic upon bivalves and polychaetes; a few of the larger species are apparently free-living in sandy substrates, but there are no details available of their diets.

In summary, by comparison with living gastropods, the most abundant trophic category in the Blackdown Greensand (Table 2) is the detritivores and algal feeders (44% of individuals), followed by predators and carnivores (28%), and suspension feeders (18%). By far the most abundant trophic group of the carnivores is that of the polychaete feeders, which comprises over half (51%), with that of the mollusc feeders forming 25% and

TABLE 2. Presumed diets of Blackdown Greensand gastropods (see text for details)

a. Trophic classification of the Blackdown Greensand gastropod fauna

	Individuals	Percent
Algal feeders and detritivores	1,715	44
Suspension feeders	706	18
Carnivores and predators	1,086	28
Unknown (' <i>Murex</i> ' <i>calcar</i>)	380	10

b. Possible diets of the carnivorous and predatory gastropods

	Individuals	Percent
Polychaete feeders (Acteonidae and Fasciolaridae)	554	51
Drilling of molluscs (Naticacea and Muricidae)	268	25
Mollusc feeding (<i>Tantunia</i> and <i>Cylichna</i>)	8	1
Anthozoans (Epitoniidae)	35	3
Microzoobenthos (Ringiculidae)	79	7
Parasitic ? (<i>Lacrimiformia</i>)	24	2
Unassigned (non-drilling naticids and other gastropods)	118	11

feeders upon the microbenthos amounting to 7%. The percentage of the fauna that we could not assign (11%) includes the non-drilling naticaceans and a few neogastropods.

The sandy fauna occurring in the Blackdown Greensand is similar in composition to other Albian sandy faunas known from north-west Europe (Marlière 1939; de Lorient 1882); there are also diverse marine mud faunas of similar age, which have particular elements in common. In present-day, sublittoral sandy benthic communities, polychaetes are usually the most abundant macro-invertebrate group and in the few soft-substrate gastropod assemblages that have been studied, polychaete feeders form the major trophic category (Taylor, in press).

DRILLING PREDATION

Predation holes made by gastropods can be distinguished from holes in shells by other predatory and non-predatory organisms (see cautionary review by Bromley 1981). Examples of the holes made by living naticid and muricid gastropods were used as the basis for the recognition of predation in the Albian specimens. Any doubtful holes were rejected from the analysis. It is probable that a proportion of these holes were authentic gastropod drills, but altered by taphonomic processes and therefore to a small degree we have underestimated predation rates.

The living nudibranch *Okadaia elegans* from the western Pacific can make drill holes resembling those of *Natica* in small polychaete tubes (Young 1968; figure in Kay 1979) and Bromley (1981) raised the possibility that nudibranchs existing in the past, but which have left no trace of their occurrence, may have caused some of the drill holes in fossil molluscs. This, of course, is feasible, but *Okadaia* is very small (0.6–4.0 mm), the holes it produces are very small, and it is the only nudibranch known both feeding on polychaetes and having a drilling habit (Todd 1981). Additionally, no nudibranchs are known that feed upon shelled molluscs. The existence of Albian nudibranchs is not testable, but this possibility has to be kept in mind. Opisthobranchs with reduced shells that may be nudibranch precursors are, however, not known before the lower Cainozoic (Zilch 1959).

Secondly, a distinction must be made between the holes made by naticid and muricid gastropods. The features of the drilled holes produced by the two families have been extensively documented and illustrated (Fretter and Graham 1962; Carriker and Yochelson 1968; Sohl 1969; Fischer 1922; Hoffman *et al.* 1974; Robba and Ostinelli 1975; Ziegelmeier 1954; Carriker and van Zandt, 1972; Bromley 1981). Typically, naticid holes are wide exteriorly and narrow internally with a countersunk rim ('truncated paraboloid' of some authors); muricid holes are, by contrast, straight-sided, slightly conical or cylindrical in form. However, in both these gastropod families the shape of the hole they produce may vary considerably with different prey, or its position on the shell. In certain cases the identification of the shell driller may not be possible. Naticid drillings, for instance, into the bivalve *Corbula* tend to be nearly cylindrical, but broad in the outer shell layer and somewhat narrower through the inner layer, thereby producing a stepped appearance (Ziegelmeier 1954). Such borings can resemble those made by muricids as Hoffman *et al.* (1974) noted, and in some earlier studies (Taylor 1970; Kojumdjieva 1974) these borings have been wrongly assigned.

It must be borne in mind that a proportion of prey eaten by naticids and muricids need not be drilled. Naticids are known to eat *Ensis* and small Tellinidae without drilling (Turner 1955; Vermeij 1980), and some muricids eat gastropods through the aperture, or in the case of limpets by prising them off the rocks (Taylor 1976), or bivalves by inserting their proboscis between the valves (Broom 1982).

Lever and Thijssen (1968) have shown that drilled and undrilled shells differ in their hydrodynamic properties and post-mortem transportability. However, their studies were carried out on intertidal sandy beaches, where shell transport can be considerable, but in sublittoral habitats such transport is usually greatly reduced (Warne 1969; Ekdale 1977). In the Blackdown Greensand habitat, we have assumed that drilled and undrilled shells had the same probability of preservation.

Predation upon bivalves

Eighty-three species from twenty-three superfamilies, comprising some 6,885 valves, representing 3,442 individual bivalves, were recorded in our examination of the Blackdown Greensand fauna. Thirty-six of these species are uncommon and only represented by ten, or fewer, valves. Table 3 shows the ranked abundance of the various families (3*a*); and the ten most abundant species of bivalve in the fauna (3*b*; see also text-fig. 5).

The two commonest species *Corbula elegans* and *Nicaniella formosa* are both small molluscs (4.8 mm and 3.6 mm respectively). Most of the bivalves in the fauna are shallow-burrowing in habit and these comprise 79% of individuals, with species in the Glycymerididae, Trigoniidae, Veneracea, Corbulidae, and Arctidae as the dominant elements (Table 3). Thinner-shelled, deeper burrowers from the Tellinacea, Solenacea, and Pholadomyacea form a mere 2% of the total individuals, but it is likely that members of this group are less well preserved and under-represented in collections.

TABLE 3
a. Ranked abundance and diversity of bivalves in the
Blackdown Greensand fauna by family or superfamily

	Valves	Species
1. Corbulidae	857	2
2. Trigoniidae	646	6
3. Glycymerididae	627	2
4. Arcacea	620	4
5. Astartidae	571	3
6. Veneracea	559	5
7. Nuculacea	414	4
8. Gryphaeidae	386	2
9. Mytilacea	353	6
10. Cardiacea	335	6
11. Arctidae	325	4
12. Tellinacea	253	5
13. Pteriacea	229	7
14. Nuculanacea	220	2
15. Mactracea	158	2
16. Pectinacea	118	7
17. Lucinacea	97	4
18. Poromyacea	57	1
19. Pholadomyacea	39	3
20. Limacea	10	4
21. Pinnacea	6	1
22. Thraciacea	4	2
23. Solenacea	1	1

b. Ranked abundance of the most common bivalve species

	Valves
1. <i>Corbula elegans</i>	712
2. <i>Nicaniella formosa</i>	552
3. <i>Glycymerita umbonata</i>	425
4. <i>Idonearca glabra</i>	395
5. <i>Amphidonte obliquata</i>	375
6. <i>Nucula antiquata</i>	224
7. <i>Nanonavis carinatus</i>	220
8. <i>Glycymerita sublaevis</i>	202
9. <i>Callistina plana</i>	201
10. <i>Protocardia hillana</i>	200

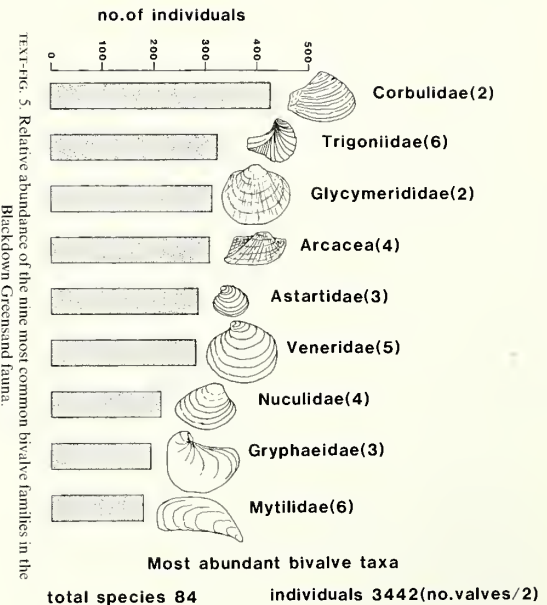
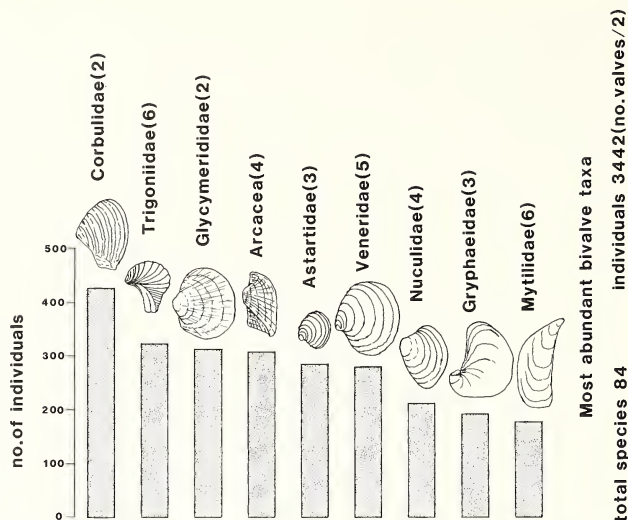


TABLE 4. Frequency of drilling by natid and muricid gastropods upon bivalves. Only the most commonly attacked species are listed here (complete data in Appendix 1)

Species	No. of drills	Percent of total drilling	No. of natid drills	Percent of natid drills	No. of muricid drills	Percent of muricid drills
<i>Corbula elegans</i>	42	18	42	28	—	—
<i>Amphidontia obliquata</i>	31	13	3	2	28	33
<i>Glycymeria umbonata</i>	26	11	15	10	11	13
<i>Nucanella formosa</i>	16	7	15	10	1	1
<i>Lionecra glabra</i>	12	5	7	5	5	6
<i>Protocardia hilliana</i>	9	4	6	4	3	4
<i>Palaeonorda thuequilis</i>	4	4	9	6	—	—
<i>Glycymeria sublaevis</i>	7	3	2	1	5	6
<i>Epicypina angulata</i>	7	3	4	3	3	4
<i>Modiolus reversa</i>	7	3	7	5	3	4
<i>Corbula truncata</i>	7	3	7	5	—	—
<i>Chionea cuperata</i>	4	2	4	3	—	—
<i>Nucula antiquata</i>	4	2	4	3	—	—
<i>Falsinurillus lanceolatus</i>	5	2	—	—	5	6
<i>Nanomavus curvatus</i>	4	2	—	—	4	5
Total drills all species	241		152		89	
Total species drilled	43		32		24	



TEXT-FIG. 5. Relative abundance of the nine most common bivalve families in the Blackdown Greensand fauna.

TABLE 4. Frequency of drilling by naticid and muricid gastropods upon bivalves. Only the most commonly attacked species are listed here (complete data in Appendix 1)

Species	No. of drills	Per cent of total drilling	No. of naticid drills	Per cent of naticid drills	No. of muricid drills	Per cent of muricid drills
<i>Corbula elegans</i>	42	18	42	28	—	—
<i>Amphidonte obliquata</i>	31	13	3	2	28	33
<i>Glycymerita unbonata</i>	26	11	15	10	11	13
<i>Nicaniella formosa</i>	16	7	15	10	1	1
<i>Idonearca glabra</i>	12	5	7	5	5	6
<i>Protocardia hillana</i>	9	4	6	4	3	4
<i>Palaeomoera inaequalis</i>	9	4	9	6	—	—
<i>Glycymerita sublaevis</i>	7	3	2	1	5	6
<i>Epicyprina angulata</i>	7	3	4	3	3	4
<i>Modiolus reversa</i>	7	3	4	3	3	4
<i>Corbula truncata</i>	7	3	7	5	—	—
<i>Chionea caperata</i>	4	2	4	3	—	—
<i>Nucula antiquata</i>	4	2	4	3	—	—
<i>Falcimyrtilus lanceolatus</i>	5	2	—	—	5	6
<i>Nanonavis carinatus</i>	4	2	—	—	4	5
Total drills all species	241		152		89	
Total species drilled	43		32		24	

Epifaunal and endobyssate bivalves comprise 19% of individuals, most common being the exogyrid oyster *Amphidonte obliquata*, the byssate arcid *Nanonavis carinatus*, mytilids, and inoceramids.

Forty-three species of bivalve are eaten by predatory gastropods, but 73% of attacks are made on eleven species (see Table 4 and Appendix 1). Eleven of these species are eaten exclusively by muricid gastropods, a further nineteen exclusively by naticids, and the remaining thirteen are eaten by both predators.

The most frequent prey drilled by muricid gastropods is the oyster *A. obliquata*, which amounts to 33% of muricid attacks, and this is followed by *Glycymerita umbonata* that has suffered 13%. As might be expected the prey of the muricids mainly consists of epifaunal and some shallow-burrowing species, which require little excavation from the substrate. Although some twenty-four species of bivalve are drilled by muricids, 69% of these attacks are made on only six species with 46% occurring on just two species.

The principal species of bivalve drilled by naticid gastropods is the small *C. elegans* which forms 28% of attacks, with *G. umbonata* and *Nicaniella formosa* each undergoing 10% of attacks. A total of thirty-two species are drilled by naticids, but 77% of all their predation occurs upon eleven species, all of which were probably burrowers, except for *Modiola reversa* that is thought to have been endobyssate, and a few drills occurring in the epifaunal *Amphidonte*.

Some prey are drilled by both naticid and muricid gastropods. The most notable of these are *G. umbonata*, *Protocardia hillana*, *Epicypina angulata*, and *M. reversa*. The majority of these shared prey species are very shallow burrowers, or else endobyssate in habit and therefore available to both predators. A few naticid holes were observed in the lower cemented valve of *A. obliquata*; this small oyster lived attached to shell fragments on the sandy substrate and may have been occasionally taken in a manner similar to the irregular predation of the Recent *Polinices duplicatus* upon the epifaunal byssate *Mytilus edulis* (Edwards 1974).

Predation upon gastropods

We have recorded some 3,894 gastropod specimens representing the occurrence of sixty-five species in the Blackdown fauna (Table 1 and Appendix 2). The great majority of these species are uncommon and, in fact, five species account for 69% of the total individuals. By comparison with their living relatives, most of these more abundant species are considered to be shallow burrowers, or surface ploughers on soft substrates.

Twenty-three species of gastropods are drilled by naticids and four by muricids, with all of that four being drilled by both predators. The naticids are responsible for most of the predation upon gastropods (92%) with that by the muricids amounting to the remaining 8%. The ranked total predation by species is shown in Table 5 with the four species *Drepanocheilus calcarata*, *D. neglecta*, '*Murex*' *calcar*, and *Turritella granulata* suffering 74% of the attacks made by both of these predators. The same four prey species form 75% of naticid predation and also the greater part of that by the muricids.

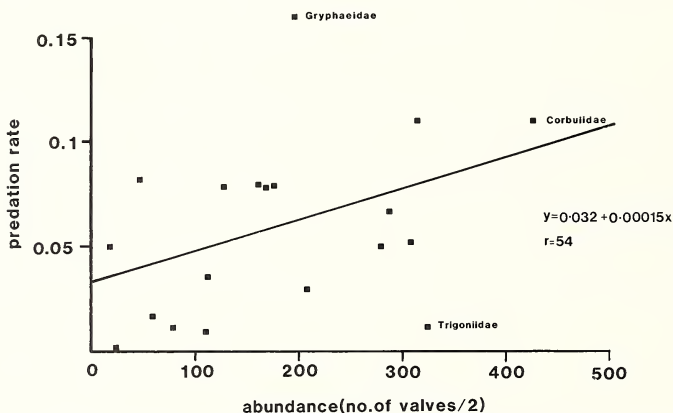
Prey preferences

Kitchell *et al.* (1981) have recently provided a model for prey selection by naticid gastropods based upon a cost-benefit analysis of the different prey types. Although this approach, which they have applied to an analysis of predation by naticids on Miocene *Glycymeris*, is of considerable interest, we do not consider that the method is appropriate for the Blackdown Greensand fauna. The reasons for this are first, the low predation rate, and secondly, our lack of precise knowledge as to the natural abundance of the prey species. However, bearing in mind the limitations of the samples used in our own study, we can make some simple analyses of prey preferences.

If we compare predation rate against the relative abundance of bivalve families (text-fig. 6), then there is a significant (2% level) positive correlation with increasing abundance, reaching a peak in the Corbulidae. Conspicuous exceptions of this trend are found in the Gryphaeidae, which are drilled at a higher rate than their abundance would suggest, and in the Trigonidae which are ranked second

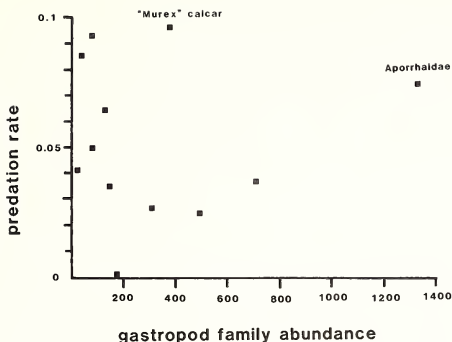
TABLE 5. Gastropod species most commonly drilled by predatory gastropods. Complete data in Appendix 2

Species	Total drilling	Per cent	Naticid drilling	Per cent	Muricid drilling	Per cent
<i>Drepanocheilus calcarata</i>	49	23	43	22	7	44
<i>D. neglecta</i>	50	24	46	24	3	19
' <i>Murex</i> ' <i>calcar</i>	37	18	32	16	5	31
<i>Turritella granulata</i>	26	12	26	13	—	—
' <i>Littorina</i> ' <i>conica</i>	8	4	8	4	—	—
<i>Tornatellaea affinis</i>	7	3	7	4	—	—
<i>Margarites monilifera</i>	5	2	5	3	—	—
<i>Avellana incrassata</i>	4	2	4	2	—	—
<i>Forator parkinsoni</i>	4	2	4	2	—	—
<i>Confusiscala fittoni</i>	3	1	3	2	—	—
<i>Gyrodes gentii</i>	2	1	2	1	—	—
<i>Pictavia rotundata</i>	2	1	2	1	—	—
<i>Tornatellaea</i> cf. <i>cosnensis</i>	2	1	2	1	—	—
<i>Blackdownia quadrata</i>	2	1	2	1	—	—
Total individuals drilled	211		195		16	
Total species drilled	23		23		4	



TEXT-FIG. 6. Relation of predation rate and family abundance for bivalves in the Blackdown Greensand fauna (Gryphaeidae and Trigoniidae excluded from regression analysis for reasons given in text).

in abundance, but have a very low predation rate. The explanation for this would seem to be that five of the six species of Trigoniidae in this fauna are thick-shelled and have a highly rugose shell ornament; they were also probably capable of a leaping movement in order to avoid predation as has been described by Stanley (1977a) for their living relatives. The oyster *Amphidonte* is the only really common epifaunal bivalve available to the muricids and it would have ranked first in accessibility to



TEXT-FIG. 7. Relation of predation rate and family abundance for gastropods in the Blackdown Greensand fauna.

them. Moreover, comparison with present-day oysters would suggest that the Albian oysters were locally aggregated, thereby increasing their local abundance.

For the gastropods (text-fig. 7) high predation rates are found amongst some of the least abundant families. Out of the more numerous taxa, '*M.* *calcar*' has the highest predation rate followed by the Aporrhaidae. Of the latter family *D. calcarata* is three times more abundant in our samples than is *D. neglecta*, but it has a predation rate of 5.1% which is significantly lower (chi square $p < 0.001$) than that of *D. neglecta* (18.2%). This indicates that if the relative abundance in our samples reflects the natural (living) frequency of the two species, then *D. neglecta* is being actively selected by the predators.

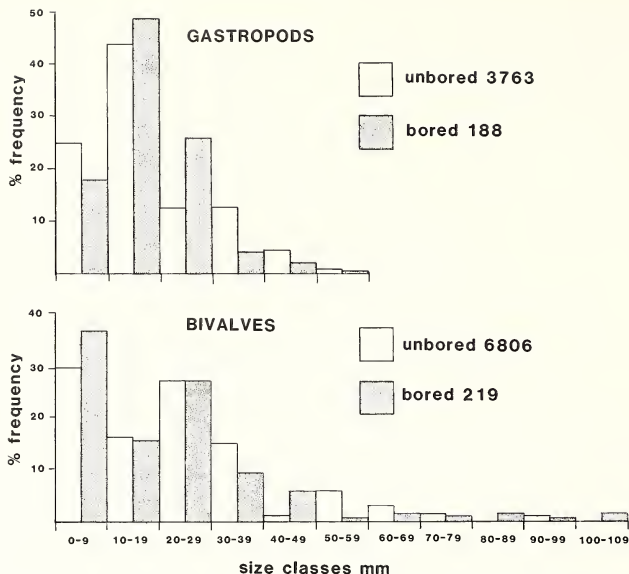
Perron (1978) has reported a marked seasonal change in the behaviour of living *Aporrhais occidentalis* (which probably also occurs in *A. pespelecani*), that would affect their availability to predators. The gastropods remain burrowed and quiescent from August until February but active on the sediment surface from February to late summer—although there is some variation in the length of this active period dependent upon sex and maturity. Such behavioural characteristics ought to be borne in mind when interpreting results obtained from fossil assemblages.

Our results tentatively suggest that the predators are tending to select the most abundant bivalve families, but avoiding the Trigoniidae. They also seem to be preferentially selecting the gastropods '*M.* *calcar*' and *D. neglecta*. It must be stressed that these data are based upon abundance in museum collections.

Size of prey

Living naticid gastropods show strong size selection of prey (Ansell and Mace 1978a; Kitchell *et al.* 1981), but we were unable to detect such behaviour in our admittedly small samples.

The size frequency distribution of the bivalves occurring in the Blackdown fauna is shown in text-fig. 8. The majority of the bivalves in the various assemblages (72%) are between 4 and 30 mm in length. The preponderance of small individuals is largely due to the great abundance of *C. elegans* and *N. formosa*. The sizes of the bivalves drilled show a very similar size distribution, with 79% of the individuals taken being between 4 and 30 mm. There was no significance difference (chi squared) between the sizes of the populations. For the most frequently drilled species, *G. umbonata*, *Amphidonte obliquata*, and *C. elegans*, there were similarly no significant differences (*t* test) between the sizes of drilled and undrilled shells.



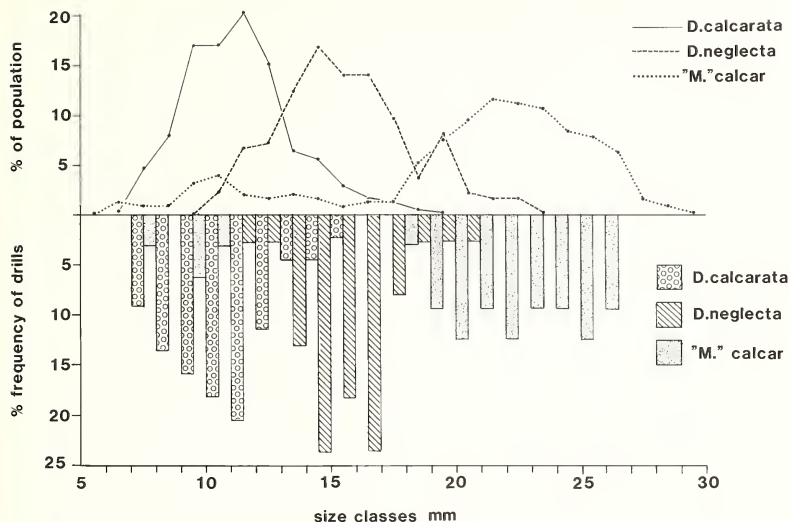
TEXT-FIG. 8. Comparison of the size frequency distributions of drilled and undrilled molluscs in the Blackdown Greensand fauna.

Taking the bivalve assemblage as a whole, the muricids drill significantly larger (t test $p < 0.001$) bivalves (mean shell length = 29.5 ± 18.2 mm, $n = 75$) than naticids (= 17.3 ± 18.5 , $n = 144$). In the case of *G. umbonata* which was attacked by both naticid and muricid predators, those eaten by muricids (shell length = 22.3 ± 6.6 mm, $n = 7$) were not significantly larger than those taken by naticids (16.9 ± 4.9 mm, $n = 15$).

For gastropods the majority of the individuals (80%) are in the category of 3–30 mm in shell height and the drilled shells follow the same distribution (see text-fig. 8). Comparison of the two predominant aporrhaid species (text-fig. 9) reveals that *D. neglecta* (shell height = 15.4 ± 2.9 mm, $n = 136$) is considerably larger (t test, $p < 0.001$) than *D. calcarata* (ht. = 11.5 ± 2.2 mm, $n = 166$). There are no significant differences for either species in the sizes of drilled and undrilled shells. However, the drilled shells of *D. neglecta* (15.6 ± 1.82 mm, $n = 36$) are significantly larger than those of *D. calcarata* (10.5 ± 1.95 mm, $n = 42$). The much larger aporrhaid *Perissoptera parkinsoni* (mean shell height = 37.9 mm) is not drilled by either naticids or muricids.

Drilling behaviour

The siting of drill holes in the shell may illustrate aspects of the behaviour of the predator. This evidence cannot be used to distinguish between the activities of different species of naticids, for studies of living naticids have shown that the position drilled is dependent upon the size, shape, ornamentation, and behaviour of particular prey species; which are all factors that determine how the



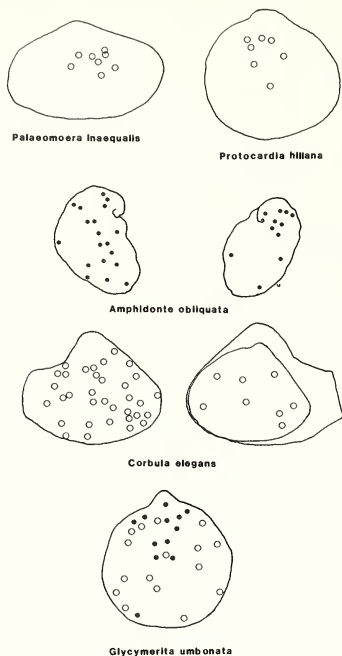
TEXT-FIG. 9. Size frequency distribution of drilled and undrilled shells for the three most heavily predated gastropod species, *Drepanocheilus calcarata*, *D. neglecta*, and '*Murex*' *calcar*.

prey will be manipulated in the foot of the predator (Ansell 1960). Nevertheless, some living naticids do have a distinctive drilling style; for instance, *Polinices tumidus* usually drills bivalves across the valve margins at the ventral commissure (Vermeij 1980).

In *C. elegans* (text-fig. 10) where the two valves differ considerably in size, there are significantly more naticid holes (50% probability test $p < 0.002$; $n = 36$) in the larger right valve, which is the lower valve in life orientation, than in the smaller left valve ($n = 8$). Such a valve preference is not found in any of the other bivalve prey species, even in the oyster *Amphidonte* where the valves differ considerably in size.

In some prey species naticid drills are frequently consistently placed, e.g. in *Palaeomoera* and *Protocardia* (text-fig. 10), indicating similar handling and orientation in the foot prior to drilling. This stereotypy of drilling behaviour (Berg and Nishenko 1975) is usually seen on the shells of burrowing bivalves. In very shallow, or small bivalves such as *Glycymerita* and *Corbula* the position of the drill hole is more variable.

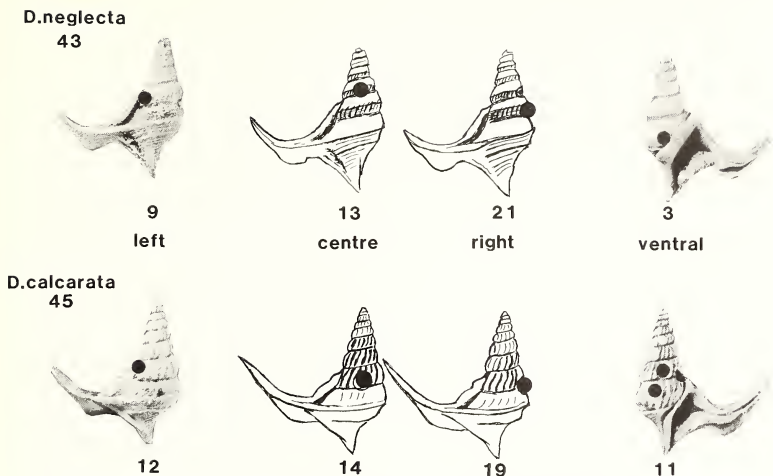
Muricid gastropods do not usually manipulate the prey with the foot, as naticids do, and the drill holes they produce tend to be more randomly positioned (Carriker and van Zandt 1972), which is exemplified by the muricid predation found in *Amphidonte* (text-fig. 10). Both naticids and muricids feed upon the surface burrower *G. umbonata*, but the muricid holes tend to be concentrated in the dorsal area of the shell, while the naticid holes are more widely dispersed. Glycymerid bivalves usually live in a near vertical, hinge-uppermost position, with the umbones at, or very near, the sediment surface (Thomas 1975). Since muricids have very limited powers for excavation of their prey, the dorsal areas of shells are the only sites available for them to drill. In contrast, naticids approach the prey within the sediment and then manipulate it in their foot.



TEXT-FIG. 10. Drill hole positions in four species of bivalves: open circles—naticid holes, solid circles—muricid holes.

Naticid drilling on gastropods also tends to be relatively stereotyped with each species tending to be drilled in a preferred position. The results of examination of the drill hole positions occurring in *D. calcarata* and *D. neglecta* are given in text-fig. 11. In both species significantly more (50% probability test) drills occurred upon the dorsal surface and although more attacks (23%) occurred on the ventral surface of *D. calcarata* compared with just 7% in *D. neglecta* this difference was not found to be significant (Yates's chi square). Most attacks on both species, whether dorsal or ventral, occurred in the second whorl (chi square $p < 0.01$). Division of the shell into three sectors (left side, central, and right side) showed that there was no significant preference for drill position between the three sectors.

Holes drilled across whorl boundaries were common in gastropods and examples of unproductive drilling into the apertural flange of aporrhoids, or occasionally the thicker varix area of other shells, were found. Instances of multiple drillings occurred; one *C. elegans* had six failed and one successful drill holes. Failed borings frequently occur in the Corbulidae (Fischer 1963; Hoffman *et al.* 1974; Ziegelmeier 1954). These failed drills often terminate at a unique organic periostracum-like layer situated between the outer and inner layers. This might be an adaptation to foil drilling predators. If so, then it was effective very early in the history of drilling predation upon the Corbulidae. A specimen of *Fossarus granosus* [Taunton Museum No. 6548] has one incomplete and five relatively complete holes, the majority of which show the typical naticid bevel. This probably indicates repeated



TEXT-FIG. 11. The positions and frequency of drills occurring in the two species of *Drepanocheilus*.

disturbance and dislodgement of the predator. Examples of multiple drillings arising from several individual predators drilling the same prey do not appear to occur for naticids, but are quite common with some muricids (Hughes 1980b; Taylor, pers. observation).

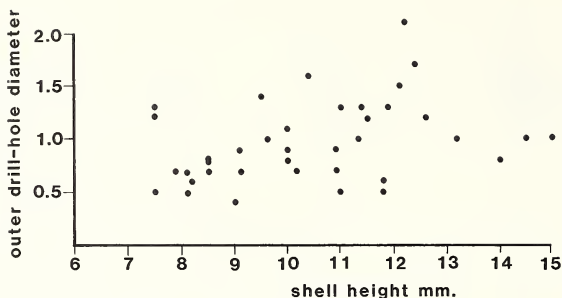
Some observations have related the size of the drill hole to the size of predator. However, for *Urosalpinx* (Muricidae), Carriker and van Zandt (1972) have shown that the diameter of the hole drilled by individual snails varied considerably according to their condition, their hunger state, and the degree of extension of the accessory boring organ. Another factor is that muricids do not need to manipulate their prey in the foot and can drill prey considerably larger than themselves.

The correlation of drill hole diameter and the size of the predator is more exact for naticids (Ansell and Mace 1978a, b; Wiltse 1980; Kitchell *et al.* 1981) although experimental observations have also indicated that both hunger state and radula wear (Ziegelmeyer 1954) influence matters. The diameter of the hole made by individual predators varies according to the nature of the prey species (Ansell and Mace 1978a, b). In the Blackdown fauna we have a wide variety of gastropod and bivalve prey eaten, but at low drilling frequencies. Consequently, it was decided that any general consideration of predator-prey size relationships would be pointless. Yet the relationship of drill hole diameter and prey size (shell height) in *Drepanocheilus* species was examined and we found that there was no correlation between the external diameter of the drill hole and prey size for either *D. calcarata* or *D. neglecta* (text-fig. 12), a result that was very different from the high correlation found for fossil *Glycymeris* by Kitchell *et al.* (1981).

Summary of the diets of drilling gastropods in the Blackdown Greensand

The main items in the diets of naticid and muricid gastropods, as deduced by the frequencies of drilled shells in the Blackdown Greensand, are shown in text-figs. 13 and 14.

The muricids drilled many more bivalves than gastropods (77%:23%) with oysters and shallow-burrowing bivalves comprising their main prey. Naticids drilled about the same number of



TEXT-FIG. 12. Plot of outer borehole diameter against prey height for *Drepanocheilus calcarata*.

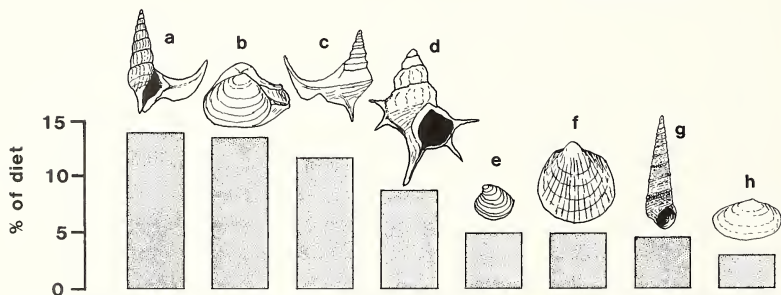
Diet of naticid gastropods

species in diet 32

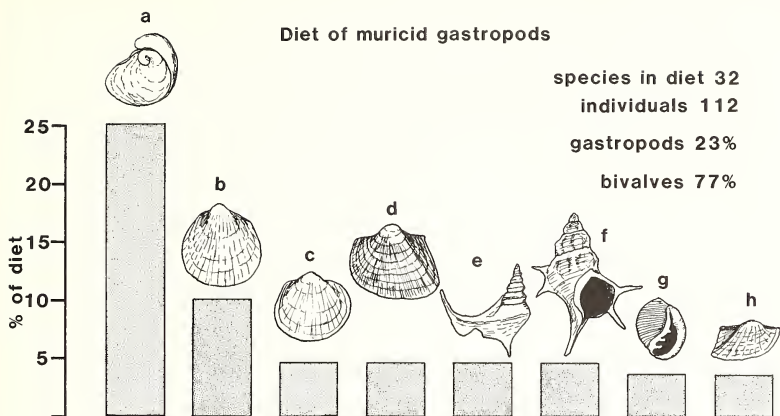
individuals 313

gastropods 51%

bivalves 49%



TEXT-FIG. 13. Percentage frequency of the eight most common prey items drilled by naticid gastropods. a, *Drepanocheilus calcarata*; b, *Corbula elegans*; c, *Drepanocheilus neglecta*; d, '*Murex*' *calcar*; e, *Nicaniella formosa*; f, *Glycymerita umbonata*; g, *Turritella granulata*; h, *Palaeomoera inaequalis*.



TEXT-FIG. 14. Percentage frequency of the eight most common prey items drilled by muricid gastropods. a, *Amphidonte obliquata*; b, *Glycymerita umbonata*; c, *Glycymerita sublaevis*; d, *Idonearca glabra*; e, *Drepanocheilus neglecta*; f, *Murex calcar*; g, *Avellana incrassata*; h, *Nanonavis carinatus*.

gastropods as bivalves (51%:49%), with their principal prey consisting of *Drepanocheilus* species, '*M.*' *calcar*, and *C. elegans*. The naticids also drilled a much greater number of prey species than muricids.

This relative balance in prey preference between gastropods and bivalves would appear to differ from the results of prey preference experiments on living *Polinices duplicatus* conducted by Wiltse (1980) and referred to by Kitchell *et al.* (1981, p. 535). In these, the preference ranking were found to be: *Mya* > *Mercenaria* > *Mytilus* > gastropods and these also coincided with what Kitchell *et al.* (1981) found to be the net profitability. Gastropods are also ranked low in the preference of the European *P. alderi* (Ansell, pers. comm.).

CONCLUSIONS

The Blackdown Greensand fauna is one of the most diverse and well-preserved Albian faunas—a time at which the major evolutionary radiation of predatory prosobranchs was beginning (Taylor *et al.* 1980). Despite the limitations imposed by the lack of current exposures, the Blackdown fauna, as recognized from museum collections, is of considerable importance in the context of this radiation, for not only are there a variety of predatory gastropods in the 'assemblage', but also associated evidence of their predatory activities. Some of the earliest muricid gastropods known to us occur in the fauna and these are accompanied by the evidence of typical muricid drill holes in the shells of molluscan prey. Similarly, the earliest drill holes known to us which can reasonably confidently be assigned to the Naticidae are found in this fauna. The results of our analyses show that, despite the fact that these are early records of predation, the prey preferences and drilling behaviour of the Albian predators were clearly very similar to those displayed by their present-day equivalents. We have no evidence to suggest that the Albian naticids and muricids were less efficient in prey capture than their modern counterparts, even though Stanton and Nelson (1980) have suggested that cannibalism and eating a wide range of prey types indicated inefficient feeding for their Eocene naticids.

TABLE 6. Percentage frequency of predation upon Turritellidae, Glycymerididae, Corbulidae, and for total gastropod and bivalve assemblages in various faunas from the Cretaceous to the Recent. Data in some cases are recalculated from the original

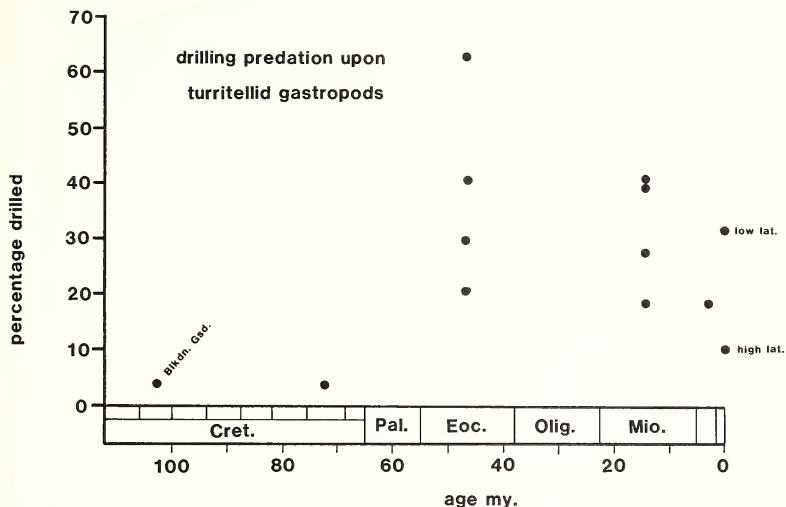
Key to symbols: a—Adegoke and Tevesz (1974), b—Dudley and Vermeij (1978), c—Fischer (1966), d—George (1965), e—Hoffman *et al.* (1974), f—Kojumdjieva (1974), g—Matsukuma (1977), h—Robba and Ostinelli (1975), i—Smith (1932), j—Taylor (1970), k—Thomas (1976), l—Vermeij (1980).

	Turritellidae	Glycymerididae	Corbulidae	All gastropods	All bivalves	Reference
Cretaceous						
Albian, England	4	10	11	5	4	herein
Campanian, U.S.A.	4					b
Eocene						
Paris Basin	21	10	28	17	26	j
Paris Basin	63	9	22	26	13	c
Nigeria	30		25	19	5	a
Miocene						
Poland	19	40	27	11	14	e
Bulgaria	40*, 41*	11	11			f
Eastern U.S.A.		27				k
Eastern U.S.A.	28					b
Pliocene						
Italy	19		16	14	15	h
Eastern U.S.A.		24				
Recent						
Guam					19	l
Plymouth		23			24	i
Japan		51, 73				g
Italy		34				d
Tropical (mean)	32					b
Temperate (mean)	11					b

* The two largest *Turritella* samples documented by Kojumdjieva (1974).

Glycymerid and corbulid bivalves, oysters, and *Turritella* are still, and were throughout the Cenozoic, important prey items of both the naticids and muricids (Ziegelmeier 1954; Hoffmann *et al.* 1974; Fischer 1966; Thomas 1976; Robba and Ostinelli 1975). Aporrhaid gastropods are one of the main items in the diet of the Albian naticids, but today that family is restricted to just two species in the Mediterranean and north-west Europe and one along the eastern coast of the U.S.A. To our knowledge there has not been a study of naticid predation upon these species, although examples of *Natica*-drilled specimens of *Aporrhais* occur in museum collections.

It has been suggested that there was a major increase in predation intensity during the late Mesozoic, which had profound effects upon the evolution of benthic invertebrates (Vermeij 1977). Drill holes produced by predatory gastropods afford one of the few methods of assessing predation intensity in fossil faunas and this reason led Dudley and Vermeij (1978) to document the drilling rates occurring in turritellid gastropods from the late Cretaceous to the present day. They concluded that the frequency of drilling had remained about the same from the Eocene until the present, but that there had been a marked increase from the late Cretaceous to the Eocene. Our data from the Black-



TEXT-FIG. 15. Percentage frequency of predation on turritellid gastropods from various faunas from the Cretaceous to Recent. Data from Table 6.

down Greensand giving a 3.7% drilling frequency for *Turritella* are remarkably similar to the 3.8% recorded by Dudley and Vermeij (1978) from the Campanian–Maastrichtian. Further data from the Cenozoic (Table 6) corroborate their findings that Cenozoic drilling rates upon *Turritella* were at least four or five times greater than had occurred in the Cretaceous (text-fig. 15).

We have also extracted comparable data for glycymerid and corbulid bivalves, that were abundant in the Blackdown fauna and are prominent in published accounts of Cenozoic drilling predation (Table 6). In the Glycymerididae, Albian predation rates (10%) are similar to those of the Eocene, but most post-Eocene rates are much higher (24% and above). The drilling rates in Eocene Corbulidae are about double those of the Albian but samples from post-Eocene faunas are rather limited.

When the few complete assemblages that have been analysed are compared (Table 6), it is found that the overall drilling rates on gastropods and bivalves are two to three times higher in the Cenozoic than in the Cretaceous. The predation rate of bivalves for the Eocene of Nigeria (Adegoke and Tevesz 1974) is lower than for other Cenozoic faunas and this led those authors to suggest that there had been a shift in prey preference by predators from mainly gastropods in the Eocene to predominantly bivalves at the present day. It would appear that this conclusion was based upon inadequate sampling and, perhaps, an anomalously low predation rate upon the bivalves in their fauna. To our knowledge, there are no accounts of Recent assemblages that have been analysed in the same way as the fossil faunas; Reyment (1966) examined a fauna from the Niger delta, but did not provide full details, nor give sample sizes.

Thus, both with regard to individual taxa and total assemblages, our data support the hypothesis that there has been a marked increase in drilling predation from the Cretaceous to the Cenozoic and that predation rates throughout the Cenozoic have probably been similar to those of the present day.

However, as Vermeij (1980) pointed out, there is likely to be considerable variation in predation intensity at any one time, depending upon the abundance of drilling predators, and it is apparent that such molluscs were certainly not very abundant during the Albian.

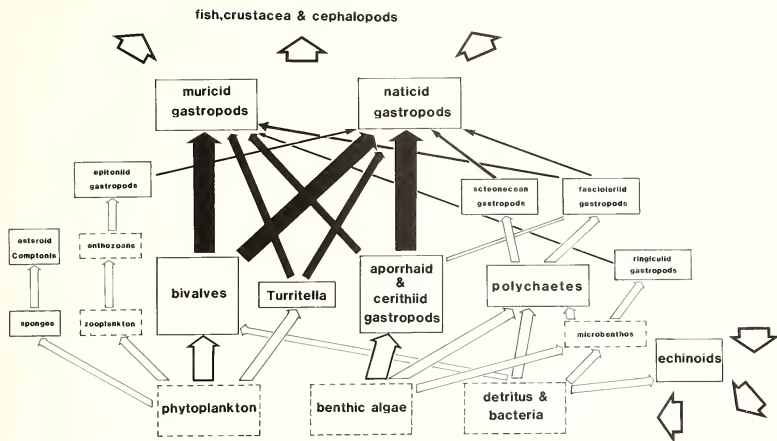
The increased success and efficiency of predators generates selection for defence mechanisms in the prey, which in turn cause selection for predation mechanisms to overcome the defences. This escalating arms race between predators and their prey has been discussed recently (see reviews by Hughes 1980a; Bayne 1981) while details of the refugia sought by the prey and the evolutionary response caused in the predator-prey interaction have been examined by Kitchell *et al.* (1981). The adaptations used by prey will tend to be morphological, chemical, or behavioural. These will include escape reactions; camouflage by colour, or morphology; selection of cryptic habitats, or living positions out of reach of the predator; patchy, or other dispersed distributions; refuge through growth beyond that likely to succumb to a successful attack by the predator; and morphological armament reducing the efficiency of attack. Some of the possible responses of prey species to the increased activities of predators in the late Cretaceous have been discussed by Stanley (1977b), Vermeij (1977), and Taylor (1981). These included on the positive side: deeper burrowing in bivalves, strengthening and armament of shells, habitat shifts; or the negative consequence of ultimate extinction. A size refuge from predation has been widely reported. In one study on *Mya arenaria*, Edwards and Huebner (1977) have demonstrated that although small and medium-sized *Mya* are heavily predated by *Polinices duplicatus*, larger individuals are seldom attacked; the reproductive reservoir of these larger molluscs which cannot be handled by *Polinices* is sufficient to maintain the *Mya* population. Similarly, Ansell (1960) found that *P. alderi* did not attack *Chamelea striatula* at sizes much above 15 mm.

Oysters are a major prey of muricid gastropods, both in the Albian and the Eocene of the Paris Basin (Taylor 1970). Both of these faunas represent sublittoral marine habitats with no evidence of other than normal salinities. However, at the present day, large populations of oysters are found in reduced or fluctuating salinity conditions, or in the intertidal zone. It is suggested that both of these habitats represent a refuge from the intense predation pressure of normal sublittoral habitats; fewer predators live in either reduced salinity, or intertidal habitats. A number of studies have demonstrated reduced feeding and reproductive activity in muricid gastropods in conditions of reduced or fluctuating salinities (reviewed in Broom 1982). At the present day most large populations of epifaunal bivalves are found in the intertidal, low salinity, or cryptic habitats, or alternatively have some adaptations such as swimming abilities (Pectinidae), or have an association with coelenterates (e.g. Pteriidae) that reduces predation intensity. By contrast, during the Cretaceous, sublittoral populations of these epifaunal bivalves including inoceramids, rudists, oysters, modiolids, and pteriids were abundant.

Although mollusc species with thick shells, strong sculpture, and tight closure might be expected to show lower drilling frequencies, no such correlation has been consistently established (Vermeij 1980). It might be thought that the low drilling frequencies occurring in the very abundant, strongly sculptured thick shells of the Blackdown Greensand Trigoniidae offered support for this contention. However, these trigoniids were probably capable of leaping actions to avoid predators, comparable to that shown by the living *Neotrigonia* and some Cardiidae (Stanley 1977a; Ansell 1969).

It is difficult to use drilling frequencies as an estimate of the contribution made by drilling predators to total prey mortality because other forms of predation can remove shells from the population, e.g. crushing predators. Green (1968) reported that although 22% of *Notospisula* shells were drilled by naticids, the snails only contributed to some 4% of the total annual mortality of the bivalves, 28% of which resulted from skate predation.

Therefore, it would seem clear that with drilling rates of only 4-5%, the predatory gastropods were not a particularly important influence in the mortality of benthic molluscs in the Blackdown Greensand fauna. It is most likely that fish and crustacea were far more important predators upon the fauna, but neither group has been preserved although both are common in other contemporaneous Albian deposits.



TEXT-FIG. 16. Diagrammatic reconstruction of the part of the benthic food web involving shell-drilling gastropods for the Blackdown Greensand fauna. Solid arrows indicate direct evidence of feeding relations; open arrows indicate inferred pathways. Boxes enclosed by solid lines indicate presence of fossils, dashed lines indicate inferred presence.

In order to summarize our interpretation of the Blackdown Greensand fauna, we have attempted to reconstruct part of a food web that involves the predatory gastropods (text-fig. 16). The construction of food webs for fossil faunas, obviously, has considerable limitations, in particular the inevitable lack of preservation of a large part of the fauna (see Stanton and Nelson 1980 for discussion), but it does emphasize the dynamic relationships and linkage between the various components. Our postulated food web is based upon the preserved predation evidence, a comparison with living relatives for all faunal elements, and the extrapolation of existing food webs. An instance of the evidence used can be demonstrated by the unit: all living epitoniid gastropods for which a diet is known feed upon anthozoans, these in turn feed upon zooplankton, which themselves feed upon the phytoplankton. Other units are based on similar comparisons: the asteroid *Comptonia* occurring in the Blackdown fauna belongs to the order Valvatida, Recent species of which feed upon sponges (Sloan 1980); acteonacean gastropods today feed upon polychaetes, but only a few tubicolous species are found fossil and these must represent a small fraction of the presumably prolific original fauna.

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APPENDIX 1

List of Bivalvia from the Blackdown Greensand and the incidence of drilling predation

	No. of valves V	No. of naticid drills N	No. of muricid drills M	Total no. of drills T
Nuculanacea				
<i>Mesosacella angulata</i> (J. de C. Sowerby)	50	2	—	2
<i>M. lineata</i> (J. de C. Sowerby)	170	1	—	1
Nuculacea				
<i>Nucula antiquata</i> (J. de C. Sowerby)	224	4	—	4
<i>N. impressa</i> (James Sowerby)	143	—	1	1
<i>N. pectinata</i> J. de C. Sowerby	7	—	—	—
<i>N. obtusa</i> J. de C. Sowerby	40	1	—	1
Arcacea				
<i>Nanonavis carinatus</i> (James Sowerby)	220	—	4	4
<i>Barbatia rotundata</i> (J. de C. Sowerby)	4	—	—	—
<i>Idonearca glabra</i> (Parkinson)	395	7	5	12
<i>Trigonarca passyana</i> (d'Orbigny)	1	—	—	—
Limopsacea				
<i>Glycymerita sublaevis</i> (J. de C. Sowerby)	202	2	5	7
<i>G. unibonata</i> (James Sowerby)	425	15	11	26
Mytilacea				
<i>Falcimythilus lanceolatus</i> (J. de C. Sowerby)	42	—	5	5
<i>Musculus striatocostatus</i> (d'Orbigny)	8	—	—	—
<i>Modiolus reversa</i> J. de C. Sowerby	148	4	3	7
<i>Perna</i> 'inaequivalvis' J. de C. Sowerby	6	—	—	—
<i>Crenella bella</i> J. de C. Sowerby	2	—	—	—
<i>C. orbicularis</i> (J. de C. Sowerby)	147	1	1	2

	No. of valves V	No. of naticid drills N	No. of muricid drills M	Total no. of drills T
Pteriacea				
<i>Inoceramus concentricus</i> (Parkinson)	156	—	—	—
<i>I. subsulcatus</i> Wiltshire	7	—	—	—
<i>I. sulcatus</i> Parkinson	6	—	—	—
<i>Gervillia forbesiana</i> d'Orbigny	5	—	—	—
<i>Gervillella sublanceolata</i> (d'Orbigny)	37	—	1	1
<i>Bakevillia rostrata</i> (J. de C. Sowerby)	15	—	3	3
' <i>Pseudoptera</i> ' <i>anomala</i> J. de C. Sowerby	3	—	—	—
Pectinacea				
<i>Neithea gibbosa</i> (Pulteney)	53	—	—	—
<i>N. quinquecostata</i> James Sowerby	1	—	—	—
<i>Camptonectes milleri</i> (J. de C. Sowerby)	46	—	1	1
<i>Mimachlamys robinaldinus</i> (d'Orbigny)	12	—	—	—
<i>Chlamys stutchburianus</i> (J. de Sowerby)	2	—	—	—
<i>C. elongata</i> (Lamarck)	2	—	—	—
<i>Spondylus striatus</i> (James Sowerby)	2	—	—	—
Pinnacea				
<i>Pinna robinaldina</i> (d'Orbigny)	6	—	1	1
Limacea				
<i>Lima elongata</i> J. de C. Sowerby	1	—	—	—
<i>L. subovalis</i> J. de C. Sowerby	5	—	—	—
<i>L. tecta</i> (d'Orbigny)	1	—	—	—
<i>Limatula fittoni</i> (d'Orbigny)	3	—	1	1
Ostreacea				
<i>Amphidonte obliquata</i> (Pulteney)	375	3	28	31
<i>Acutostreon</i> sp.	11	—	—	—
Trigoniacea				
<i>Pterotrigonia aliformis</i> (Parkinson)	189	—	—	—
<i>P. scabricola</i> (Lycett)	157	—	—	—
<i>Rutitrigonia eccentrica</i> (Parkinson)	138	1	1	2
<i>Oistotrigonia spinosa</i> (Parkinson)	19	—	—	—
<i>Quadratrigonia daedala</i> (Parkinson)	48	—	2	2
<i>Q. spectabilis</i> (J. de C. Sowerby)	95	—	—	—
Lucinacea				
' <i>Lucina</i> ' <i>pisum</i> J. de C. Sowerby	71	1	—	1
' <i>L.</i> ' <i>downesi</i> Woods	8	1	—	1
<i>Mutiella canaliculata</i> (J. de C. Sowerby)	17	2	—	2
<i>Lucina</i> sp.	1	—	—	—
Crassatellacea				
<i>Nicaniella formosa</i> (J. de C. Sowerby)	552	15	1	16
<i>Eriphyla striata</i> (J. de C. Sowerby)	17	1	2	3
<i>Astarte impolitum</i> (J. de C. Sowerby)	2	—	—	—
Cardiacea				
<i>Granocardium proboscideum</i> (James Sowerby)	42	—	3?	3
<i>Protocardia querangeri</i> (d'Orbigny)	2	—	—	—
<i>P. hillana</i> (James Sowerby)	200	6	3	9
<i>Thetis laevigata</i> (James Sowerby)	88	3	1	4
<i>Globocardium</i> sp.	2	—	—	—
<i>Unicardium</i> sp.	1	—	—	—

	No. of valves V	No. of naticid drills N	No. of muricid drills M	Total no. of drills T
Maत्रaceae				
<i>Maत्रa angulata</i> J. de C. Sowerby	156	1	—	1
<i>Maत्रa</i> sp.	2	—	—	—
Arcticaceae				
<i>Venilicardia cuneata</i> (J. de C. Sowerby)	153	—	2	2
<i>V. lineolata</i> (James Sowerby)	95	2	1	3
<i>Epicyprina angulata</i> (James Sowerby)	76	4	3	7
<i>E. subtruncata</i> (d'Orbigny)	1	1	—	1
Veneraceae				
<i>Chimela caperata</i> (J. de C. Sowerby)	189	4	—	4
<i>Callistina plana</i> (James Sowerby)	201	3	—	3
<i>Flaventia ovalis</i> (J. de C. Sowerby)	66	3	—	3
<i>Paraesa faba</i> (J. de C. Sowerby)	61	3	—	3
<i>Calva subrotunda</i> (J. de C. Sowerby)	42	1	—	1
Tellinaceae				
<i>Palaeomoera inaequalis</i> (J. de C. Sowerby)	183	9	—	9
? <i>Linearia striatuloides</i> (Stoliczka)	39	1	—	1
<i>Linearis subtenuistriata</i> (d'Orbigny)	26	—	—	—
<i>Icanotia siliqua</i> Casey	3	—	—	—
<i>Quenstedtia pelagi</i> (d'Orbigny)	2	—	—	—
Solenaceae				
<i>Senis</i> sp.	1	—	—	—
Myaceae				
<i>Corbula elegans</i> J. de C. Sowerby	712	42	—	42
<i>C. truncata</i> J. de C. Sowerby	145	7	—	7
Pholadomyaceae				
<i>Panopaea mandibula</i>	33	1	—	1
<i>Goniomya mailleana</i> (d'Orbigny)	4	—	—	—
<i>Myopholas</i> sp.	2	—	—	—
Thraciaceae				
<i>Periplomya</i> cf. <i>simplex</i> (d'Orbigny)	2	—	—	—
<i>Platymoida cosnensis</i> (de Loriol)	2	—	—	—
Poromyaceae				
<i>Liopistha gigantea</i> (James Sowerby)	57	—	—	—

APPENDIX 2

List of gastropods from the Blackdown Greensand and the incidence of drilling predation

	No. of shells S	No. of naticid drills N	No. of muricid drills M	Total no. of drills T
Pleurotomariacea				
Gen. and sp. indet.	1	—	—	—
Trochacea				
' <i>Jurassiphorus</i> ' <i>subornatum</i> (d'Orbigny)	2	—	—	—
<i>Margarites monolifera</i> (J. de C. Sowerby)	43	5	—	5
<i>Helicocryptus radiatus</i> (James Sowerby)	29	1	—	1
<i>Pseudoliotina</i> sp.	1	1	—	1
Cerithiacea				
<i>Cirserithium gracile</i> (J. de C. Sowerby)	122	1	—	1
<i>Bathraspira brightoni</i> Abbass	6	—	—	—
<i>B. ?fouadi</i> Abbass	1	—	—	—
<i>B. ?almadi</i> Abbass	1	—	—	—
<i>Ageria costata</i> (J. de C. Sowerby)	29	—	—	—
<i>Orthochetus</i> sp.	5	—	—	—
<i>Seila iglali</i> Abbass	3	—	—	—
<i>Uchauxia badri</i> Abbass	1	—	—	—
<i>Cerithiella devonica</i> Abbass	1	—	—	—
? <i>Exechocirsus</i> sp. nov.	1	—	—	—
Cerithiacea ?gen. nov. 1	1	—	—	—
Cerithiacea ?gen. nov. 2	1	—	—	—
? <i>Rhynchocerithium orbignyi</i> (Briart and Cornet)	2	—	—	—
Turritellidae				
<i>Turritella</i> (<i>Torquesia</i>) <i>granulata</i> J. de C. Sowerby	704	26	—	26
<i>Turritella</i> sp.	2	—	—	—
Epitoniacea				
<i>Pyrgiscus woodwardi</i> Gardner	2	—	—	—
' <i>Scalaria</i> ' <i>pulchra</i> J. de C. Sowerby	2	—	—	—
<i>Confusiscala fittoni</i> Gardner	31	3	—	3
Rissoacea				
<i>Urceolabrum queeni</i> (Gardner)	6	—	—	—
? <i>Turboella</i> sp.	1	—	—	—
?Rissoellidae sp.	2	—	—	—
' <i>Eulima</i> ' cf. <i>corneti</i> Marlière	4	—	—	—
Fossaridae				
' <i>Fossarus</i> ' <i>granosus</i> (J. de C. Sowerby)	5	6 [in 1 sp.]	—	6
' <i>F.</i> ' <i>carinatus</i> (J. de C. Sowerby)	4	—	—	—
Aporrhaidae				
' <i>Rostellaria</i> ' <i>tricostata</i> d'Orbigny	1	—	—	—
<i>Disoketa meyeri</i> Gardner	1	—	—	—
? <i>Disoketa</i> sp. nov.	1	—	—	—
' <i>Tridactylus</i> ' sp. nov. cf. <i>griffithsi</i> Gardner	2	—	—	—
<i>Pterocerella macrostoma</i> (J. de C. Sowerby)	2	—	—	—
<i>Tessarolax retusa</i> J. de C. Sowerby	4	—	—	—
<i>Perissoptera parkinsoni</i> (Mantell)	83	—	—	—
<i>Drepanocheilus neglecta</i> (Tate)	275	43	7	50
<i>D. calcarata</i> (J. de C. Sowerby)	956	46	3	49

	No. of shells S	No. of naticid drills N	No. of muricid drills M	Total no. of drills T
Vanikoridae				
' <i>Vanikoropsis</i> ' cf. <i>alsus</i> (d'Orbigny)	3	1	—	1
Naticacea				
<i>Forator parkinsoni</i> Morris and Cleavelly	189	4	—	4
<i>Gyrodontes gentii</i> (James Sowerby)	27	2	—	2
<i>G. dupinii</i> Deshayes and Leymerie	10	—	—	—
<i>Pictavia rotundata</i> (James Sowerby)	76	2	—	2
Littorinacea				
' <i>Littorina</i> ' <i>conica</i> (J. de C. Sowerby)	124	8	—	8
Uncertain family				
' <i>Murex</i> ' <i>calcar</i> J. de C. Sowerby	380	32	5	37
Muricidae				
<i>Paramorea lineata</i> (J. de C. Sowerby)	44	1	1	2
<i>Senipirum depressum</i> (J. de C. Sowerby)	4	—	—	—
<i>Culmia brighti</i> (J. de C. Sowerby)	2	—	—	—
<i>Hillites downesi</i> Morris and Cleavelly	4	—	—	—
<i>Blackdownia quadrata</i> (J. de C. Sowerby)	25	2	—	2
Fascioliariidae				
<i>Iscapulus rigidus</i> (J. de C. Sowerby)	46	1	—	1
Fascioliariidae sp. nov. cf. <i>Fusus dubius</i> (Briart and Cornet)	1	—	—	—
?Fascioliariidae				
<i>Resabulum rusticum</i> (J. de C. Sowerby)	7	—	—	—
<i>Dummonia collisnigrae</i> Morris and Cleavelly	2	—	—	—
?Melongenidae [= Galeodidae]				
<i>Tantunia clathrata</i> (J. de C. Sowerby)	6	—	—	—
?Mitridae				
Gen. et sp. indet.	1	—	—	—
?Family				
<i>Cosmia cosnensis</i> (de Loriol)	3	—	—	—
Acteonidae				
<i>Tornatellaea affinis</i> (J. de C. Sowerby)	356	7	—	7
<i>T. ebrayi</i> de Loriol	111	—	—	—
<i>T. unisulcata</i> de Loriol	16	1	—	1
<i>Tornatellaea</i> cf. <i>cosnensis</i> de Loriol	14	2	—	2
Ringiculidae				
<i>Avellana incrassata</i> (James Sowerby)	79	4	—	4
?Pyramidellacea				
? <i>Lacrimiformia pusilla</i> (J. de C. Sowerby)	21	1	—	1
<i>Lacrimiformia</i> sp. nov.	3	—	—	—
Scaphandridae				
<i>Cylichna</i> sp. cf. <i>urgonensis</i> (Pictet and Campiche)	2	—	—	—

ALLOPATRIC SPECIATION—AN EXAMPLE FROM THE MESOZOIC BRACHIOPODA

by DEREK V. AGER

ABSTRACT. The current debate on the processes of evolution is related to the author's knowledge of the phylum Brachiopoda in Mesozoic strata. An example is presented from the genus *Homoeorhynchia* in which marginal populations seem to have developed that eventually led to an ecological 'take-over' by a new species.

A GREAT deal of discussion has been going on during the past ten years about the processes of evolution. In particular there has been the alleged conflict between *phyletic gradualism* (the slow continuous process of change which has been in most palaeontologists' subconscious since the days of Darwin) and *punctuated equilibrium* (in which species are normally in a state of *stasis* or equilibrium, which is periodically punctuated or interrupted by sudden replacements of old species by new). An essential feature of the latter process is *allopatric speciation* in which the new species arise in marginal populations which have been isolated in some way from the main stable population.

Palaeontology cannot hope to tell us anything about gene flow, inherited immunities, and the rest of the matters which are under discussion at the moment, but it can provide a three-dimensional picture of evolving species which must be superior to the two-dimensional neontologists' view that has led to the current controversy over cladistics. Though I generally sympathise with the palaeontologists in this debate, I must ignore the political connotations as irrelevant and must also regret that so much emphasis has been placed on the fossil vertebrates.

Vertebrate fossils are inevitably very rare and it is unfortunate that their spectacular nature (notably among such groups as the dinosaurs) has led them to dominate the evolution debate. Even when they have been abundant enough to quantify, this has almost always been on the basis of a single unit character. Indeed, in the present debate on human evolution and the relationship between *Homo erectus* and *H. sapiens*, most of the arguments seem to concentrate on a single specimen—the Petralona skull from Greece. Not many invertebrate palaeontologists would nowadays accept a single specimen as representative of a population, let alone a whole species.

Invertebrates on the other hand, especially small marine invertebrates, are extremely abundant as fossils and in some cases are sufficiently widespread and well known to provide a meaningful picture of the nature of particular species at succeeding points in time. Thus in their survey of 'the state of the art' Gould and Eldredge (1977) could only find adequate examples of quantified evolutionary studies among the invertebrates.

Theoretically, planktonic foraminifera in continuously deposited deep-sea sediments should provide the examples needed to demonstrate such processes. My colleague Professor F. T. Banner assures me that this is so and that there is no doubt at all about phyletic gradualism in this group. He has cited numerous examples of lineages which show progressive, unidirectional, non-iterative changes (for example, in the genera *Globotruncana* and *Globorotalia*). Unfortunately few attempts seem to have been made to quantify such studies, though—as with all such studies—it would be necessary to study them throughout their area of occurrence to be sure one was dealing with evolution rather than migration. The well-known cases of reversal of coiling in *Globorotalia* as they are traced laterally across the North Atlantic provide a warning here, since clearly these are related to environmental controls. One very well-documented study has recently been published (Malmgren and Kennett 1981) in which the process of phyletic gradualism seems to be demonstrated in the lineage *Globorotalia conoidea*-*G. inflata*, though it must be noted that more than 30,000 measure-

ments of six characters were all based on material from one borehole and cannot exclude migrating factors.

If it is true that the planktonic foraminifera went on happily evolving in the open sea without punctuation and evidently without ecological isolation, then I suggest it is peculiar to planktonic forms and unlike almost all the examples I know from the fossil benthos. Presumably in their environment it is difficult to become isolated geographically or ecologically, but with the shallow water sessile benthos it is very easy.

EVOLUTION IN MARINE INVERTEBRATES

It is an elementary observation in palaeontology that some groups evolved more rapidly than others. Obvious examples of rapid evolvers are the graptolites, conodonts, and ammonoids. The most evident feature that these groups have in common is that they are all pelagic forms that moved about fairly easily in the water body. Comparable on land were the vertebrates which were equally mobile and equally rapidly evolving. On the other hand, the more slowly evolving groups in the sea were the benthos, especially sessile benthos such as brachiopods, bivalves, and corals.

Thinking in terms of allopatric speciation, the possible cause of this difference is not difficult to understand. The more mobile forms are more likely to enter marginal habitats and, given the right circumstances, to produce isolated populations in extreme conditions which may lead to the rapid evolution of new species.

If a population of giraffes is isolated in a valley where the only tree is a taller-than-average species of *Acacia*, then there will be strong selective pressure on that population to produce forms with longer necks. If circumstances change and the population is able to return to the plains from which its ancestors came, then this new stock may prove more successful in feeding than the main species and rapidly replace it. This is not Lamarckian giraffes stretching higher up the trees and passing on the ability to their offspring. It is not Darwinian giraffes all gradually evolving side by side into a new and 'better' giraffe. It is what may be called Gouldian giraffes that have done their evolving in private and then carried out a very successful take-over bid for the habitat of their ancestors. Such a process might have occurred in the Ngorongoro Crater in northern Tanzania had the giraffes been able to enter that steep-sided collapsed caldera.

Geneticists may then argue whether the rapid evolution of the marginal population was adaptation to different selective pressures or to a 'genetic revolution'. This need not concern us here since the necessary information is not available.

Gregarious sessile benthos with a short free-swimming larval stage, such as the brachiopods, are almost by definition slow evolvers. The young are of necessity adapted as closely as possible to the environment of their parents, otherwise they are very speedily selected out. There are no opportunities for 'hopeful monsters'. I cannot imagine anything in the Phylum Brachiopoda, for example, comparable to the octopuses with fifty-six and eighty-three tentacles respectively, which I have seen recently in the Toba Aquarium near Nagoya. Nevertheless, brachiopod populations are variable in their own quiet way, and this has led to a great deal of unnecessary taxonomic splitting among fossil forms. Thus Buckman (1907) created nineteen nominal species within the genus *Cincta* on the basis of material collected in one thin band in one quarry in Somerset. In my opinion, these are all referable to the species *C. numismalis* (Lamarck). Text-fig. 1 shows the variation (in one character only—that



TEXT-FIG. 1. Variation in *Zeilleria quadrifida* (Lamarck). Outline drawings of specimens in the British Museum (Natural History) from the upper Pliensbachian (*spinatum* Zone) of the Ilminster/South Petherton district of Somerset.

of valve outline) in the allied species *Zeilleria quadrifida* (Lamarck) from the Pliensbachian faunas being considered in this paper, also from Somerset. These variants range from 'typical' *Z. quadrifida* to 'typical' *Z. cornuta* (Sowerby) and both names are used equally commonly. Variation in zeilleriids generally was discussed at length by Delancey (1974). He regarded *Cincta* as a subgenus of *Zeilleria*.

So far as rates of evolution are concerned these are, of course, relative. Mesozoic brachiopods are slow compared with ammonites. They are probably fast compared with fresh-water molluscs. Maynard Smith (1981) cited five species of molluscs in Lake Turkana which changed perceptibly in a period of 50,000 years when the lake was isolated. As he said: '... 50,000 years (2 m of sediment) is sudden to a palaeontologist but gradual to a geneticist.' This detailed demonstration of 'punctuated equilibria' has now been published (Williamson 1981). However, by using ammonites as a stop-watch, the rate of evolution of Mesozoic brachiopods makes them just about susceptible to study through the blurred fossil record. It is also possible to study them over a very wide area of well-documented strata.

HOMOEORHYNCHIA

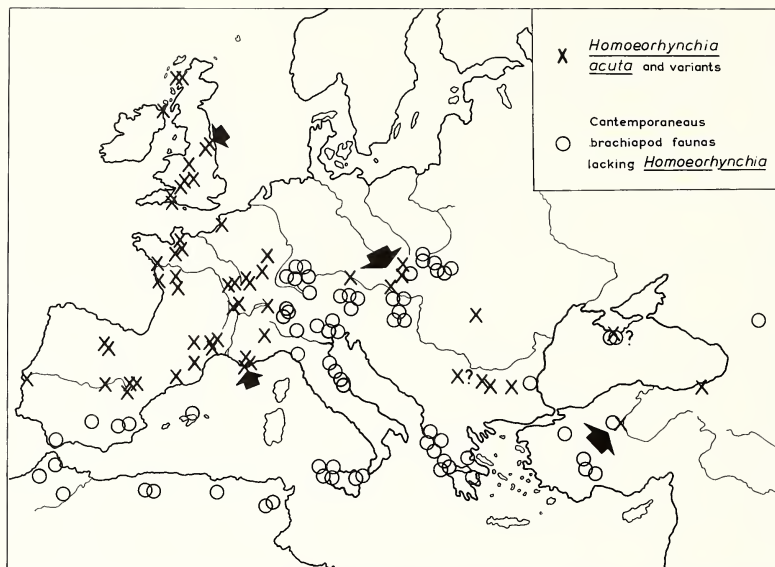
Homoeorhynchia is a well-known genus of early Mesozoic rhynchonellids. It has a trigonal form characterized by a high fold and strong, sharp uniplication in the anterior commissure. The valves are smooth with a few sharp costae appearing late in development. Internally it is a typical member of the Rhynchonellinae with radulifer crura. *Homoeorhynchia* is a particularly suitable genus for a study of this kind because its characteristically cynocephalous shape is so distinctive that it cannot easily be confused with any other form. What is more, its species are easily distinguished by means of obvious external features, whilst internally it is remarkably consistent in its main structures (Ager 1956a). It probably formed the main stock of the subfamily Rhynchonellinae from mid-Triassic to mid-Jurassic times (Ager, Childs and Pearson 1972). The distinctiveness of the various species discussed here is indicated by the slopes of the regression lines shown in text-figs. 3 to 5.

HOMOEORHYNCHIA ACUTA

Homoeorhynchia acuta (Sowerby) is a fairly uniform species, varying chiefly in lateral profile. Its outstanding characteristic is its sharp anterior plication containing a single costa. It is reasonably abundant in the upper Pliensbachian, especially in the *spinatum* Zone, right across Europe outside the Alps. It is not known outside Europe. However, it ranges from much lower in the Jurassic, notably in the Sinemurian and lower Pliensbachian, and has been recorded in the Rhaetian, though this record has not been confirmed. Closely similar earlier and probably ancestral forms are *H. ottomana* (Bittner) (e.g. specimens in the British Museum (Natural History) B 39223 from the 'Alpine Muschelkak' at Han Bulog near Sarajevo in Yugoslavia) and *H. subacuta* (Munster) (e.g. BM(NH) specimens 30646 from the 'Keuperian' of St. Cassian in Austria). It is therefore a long-ranging and stable species which virtually disappears abruptly at the top of the Pliensbachian. Text-fig. 2 shows its total known distribution. The figure also includes negative evidence in the form of records of contemporaneous brachiopod faunas where it is not known to occur.

Out of thousands of specimens I have studied of this species, I have only seen very rare variants (probably less than half a dozen) from the main populations in which a second costa is developed asymmetrically on the plication. These are so rare that they may be regarded as monstrosities, though (as is the custom) I did see fit to figure one in my monograph of British Liassic Rhynchonellidae (Ager 1956a, pl. iii, fig. 3a). This demonstrates the misleading nature of many monographs. It is probably significant, however, that it was only at the apogee of this species, when it was at its widest extent and greatest abundance at the end of Pliensbachian times, that significant marginal populations developed which were to prove its undoing.

I had no doubt until recently that *H. acuta* became extinct everywhere at the end of Pliensbachian times. I knew of no record of it anywhere in Toarcian rocks. However, in the British Museum (Natural History) I came across a small collection from the upper Toarcian that undoubtedly belongs



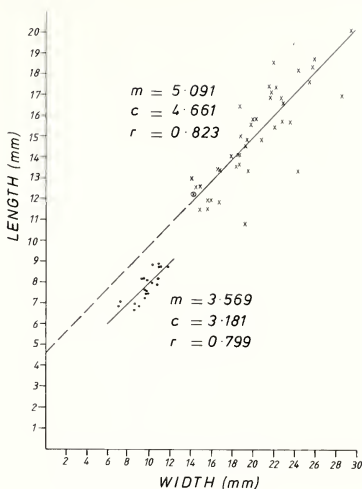
TEXT-FIG. 2. Geographical distribution of *Homoeorhynchia acuta* (shown by crosses) and contemporaneous brachiopod faunas lacking that species (shown by circles). Arrows indicate the marginal populations referred to in the text.

to this species. It was made a few years ago by Dr. M. K. Howarth and consists of twenty-three tiny specimens from the upper Lias, Moorei sub-zone of Frocester Hill, Gloucestershire (registered No. BB.45856). Dr. Howarth has confirmed (pers. comm. 1982) that there is no doubt whatever about the horizon of these specimens. Though all are very small (none larger than 9 mm in length) they are clearly adults with a well-developed uncostate plication. They do not plot in line with normal members of the species (text-fig. 3) and must be regarded as stunted survivors, living in an unfavourable environment. It is presumably significant that they occur beyond the known geographical range of *H. meridionalis*, which is not known north of Somerset.

Thus early members of *H. meridionalis* occurred in the south contemporaneously with the main body of *H. acuta* and later members of the latter species occurred in the north contemporaneously with the main body of *H. meridionalis*.

Turkish variants. These are an example of an earlier marginal population that did not get anywhere. I found this population at Yakaçık in central Anatolia, at the very edge of the known geographical range of the species. In it forms with two or three costae in the plication (the second developed asymmetrically) were not uncommon (Ager 1959, p. 1019, fig. 1). These were late Sinemurian in age and have no known descendants. All the forms here are small and poorly developed and it is reasonable to postulate marginal, rather unfavourable conditions. They fall within the normal range of variation of *H. acuta* (text-fig. 3). They appear to be very local in distribution. They were not mentioned by Vadasz (1913) who originally described Liassic brachiopod faunas from this region

TEXT-FIG. 3. Variation in *Homoeorhynchia acuta*, upper Pliensbachian Dorset and Somerset (shown by crosses) and the late Toarcian variants from Gloucestershire (shown by dots). A typical member of the Sinemurian population from Yakaçik, Turkey, is circled. m = slope of regression line; c = intercept on y axis (calculated); r = correlation coefficient. The extension of the regression line (dashes) in the upper scatter shows that the Toarcian forms are not juveniles of the normal *H. acuta*, but stunted variants. It should be noted that in this and subsequent scatter diagrams there is a slight allometry of growth which limits the significance of the regression lines.



and they do not occur in an otherwise very similar fauna I have described recently from Bilaçik, further south in Turkey (Ager *et al.* 1980).

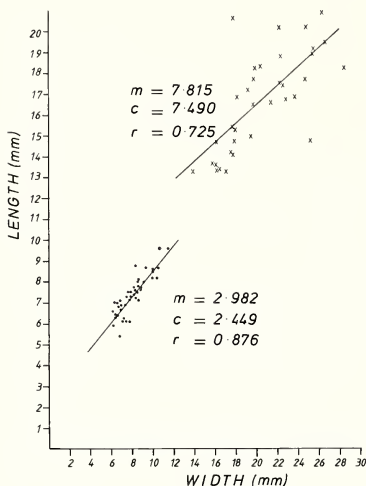
They may clearly be regarded as a marginal population, presumably at the edge of the species' range of ecological tolerance, that started to evolve in a particular direction but did not succeed. It is a clear example of an 'experiment that failed'. There may have been hundreds of such 'experiments' in the life of *H. acuta* but given the nature of the fossil record, it is fortunate that this particular one has been preserved.

Yorkshire variants. The Pliensbachian brachiopod faunas of Yorkshire have always been particularly interesting because they seem to have been cut off from the main stocks by the highly selective and probably unusual conditions of the English Midlands where ironstones were being deposited at this time. Thus the genus *Aulacothyris* is common in south-west England at this time, in the form of *A. resupinata* (Sowerby), but is completely absent from Oxfordshire up to the Humber. In Yorkshire, however, there are two further species which we may presume to have arisen through a process of geographical isolation. These are *A. pyriformis* (Tate) below and *A. fusiformis* (Rollier) above. This may also be an example of allopatric speciation (see Ager 1963, p. 258, fig. 15.5).

So far as brachiopods of a *Homoeorhynchia* type are concerned, they are virtually completely absent from the English Midlands (Ager 1956b). There are, however, two species which are—to all intents and purposes—restricted to Yorkshire. These are the tiny form of *H. capitulata* (Davidson) and the later larger form here called *H. lineata* (Young and Bird). The former may be regarded as a stunted population living in extreme conditions. It is multicostate (much more so than any of the other forms discussed herein) and only has a very short record.

The other Yorkshire species, however, was much more successful. It has commonly been placed in the genus *Rhynchonelloidea* (e.g. by Ager 1956a and 1956b) and it has differences in internal structures which make it more separate from *Homoeorhynchia* s.s. than the other populations discussed here. Nevertheless it is almost certainly not related directly to later species of *Rhynchonelloidea* (including the type species) and it seems more appropriate to link it with *H. acuta* as I did after an

'agonizing reappraisal' (Ager 1967, p. 161). It has the sharp cynocephalous fold, both in the bicostate and tricostate conditions (which were previously called '*Rhynchonella*' *bidens* and *triplicata* respectively). It is extremely common in the Yorkshire upper Pliensbachian and appears to have differed from *H. acuta* in having been able to prosper in clay ironstone depositing conditions. It does not appear to have left any descendants and the succeeding Toarcian deposits there are virtually devoid of brachiopods. Variation in *H. lineata* and *H. capitulata* is illustrated in text-fig. 4.



TEXT-FIG. 4. Variation in *Homoeorhynchia lineata* (shown by crosses) and *H. capitulata* (shown by dots), upper Pliensbachian, Yorkshire. Symbols as in text-fig. 3.

Provençal variants. Many years ago, Eudes-Deslongchamps (1863) commented that *H. acuta* was a northern form which was replaced to the south by *H. meridionalis* (a species first described by himself). When I quoted this remark in a paper (Ager 1961) I was criticized by the late and very knowledgeable specialist on Mediterranean Liassic brachiopods, G. Dubar. He did so on the grounds that Eudes-Deslongchamps had made an error in his stratigraphy and that whereas *H. acuta* was essentially a late Pliensbachian form, *H. meridionalis* belonged to the Toarcian. Dubar was, of course, basically correct, since the vast majority of the latter species—in France, in Spain, in Morocco, and even in England—belong to the early or mid Toarcian.

However, there were definite records of *H. meridionalis* in older strata in Provence. I am now told (pers. comm. Y. Almeras 1983) that all these records are incorrect and that all the Provençal forms are Toarcian in age. These again seem to be marginal populations since we are here already in the Alps and *Homoeorhynchia* is unknown in the deeper water facies not very much further east. What is more, these localities are not very far from the Toarcian localities in north-east Spain (such as Camarasa) where *H. meridionalis* becomes extremely abundant and variable.

Slovak variants. In 1964 I visited a unique locality in the Czechoslovak Carpathians with Milos Siblik. It was at Kostelec, where lower Jurassic limestones are thrust over the Cretaceous. Dr. Siblik had found an horizon, of undoubted late Pliensbachian age, with extremely abundant bicostate and tricostate cynocephalous forms. He subsequently described these as a new genus *Slovenirhynchia*

(Siblik 1967). In my view, previously expressed in a joint paper (Ager *et al.* 1972, p. 191), this is almost certainly a junior synonym of *Homoeorhynchia*. What is more, the new species named by Siblik, *S. marinensis* is, in my view, synonymous with *H. meridionalis* which does not otherwise occur in Czechoslovakia. This was also the view of Sučić-Protić (1969).

Here again we have a marginal population, close to the edge of the so-called Alpine 'trough' and indeed actually within the alpine belt, unlike any other members of the genus. What is more, it is extremely abundant, variable, and well developed. In text-fig. 2 the four localities mentioned above are all indicated with arrows and it will be seen that they are all marginal in the geographical sense. In the case of the last two localities, they are both actually in the alpine belt (where *H. acuta* does not occur) and close to much deeper water facies than those we associate with that species. It is conceivable that they represent deeper water brachiopod communities than those usually preserved in rocks of this age.

It is confidently suggested that the local, perhaps isolated, population of *Homoeorhynchia*, as seen at Kostelec gave rise to the new species *H. meridionalis* in the Toarcian, as suggested diagrammatically in text-fig. 6.

It is possible that another marginal population exists in Yugoslavia, since Sučić-Protić (1969) recorded *H. cynocephala* (Richard) and *H. crassa* sp. nov. from the middle Lias (Pliensbachian) of Serbia. These are almost certainly synonyms of *H. meridionalis* and it is noteworthy that she comments that the greatest development was in the Toarcian.

HOMOEORHYNCHIA MERIDIONALIS

As already mentioned and as implied by the specific name, Eudes-Deslongchamps regarded this species as a form of the warm south. It appears very widely in the western Mediterranean area in lower Toarcian strata. I have collected it in large numbers at such localities as Camarasa in the Spanish Pyrenees and in the Valley of Ziz in south-east Morocco. At these places it occurs in calcareous 'marls' which are quite unlike the black paper shales that one usually associates with the lower Toarcian in northern Europe. It is significant that other elements in the brachiopod fauna, such as *Spiriferina* and *Stolmorhynchia*, persist here in the south much later than they are found elsewhere. However, it is clearly not just a matter of latitude since, given the right circumstances, *H. meridionalis* can occur very much further north. The outstanding exception which proves this rule is the Ham Hill Stone in Somerset. This is a calcareous development within the Toarcian which yields abundant rhynchonellids. They were placed in a new species '*Rhynchonella*' *cynica* by Buckman (1895), by Kellaway and Wilson (1941) and by me (Ager 1956a), but again it was a matter of local specialists not recognizing a species that does not otherwise occur in their country. Variation in *H. meridionalis*, in this sense, is illustrated in text-fig. 5.

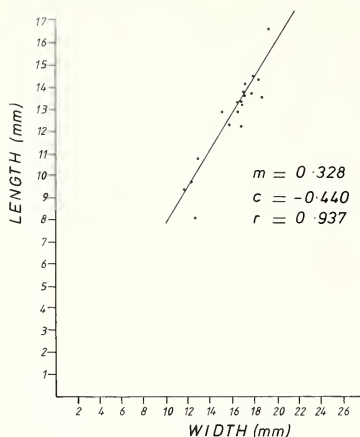
I later attributed this form to the southern species (Ager 1967, p. 161) and have no doubt that this is where it belongs. To all intents and purposes it is identical with the form found in southern Europe and northern Africa and is very well developed with no signs of stunting.

Whether or not it should be regarded as a subspecies of the better known species *H. cynocephala* (as I suggested in my recantation) is a matter of less certainty. I am persuaded by Dr. M. J. Clutson, who has worked extensively on the Toarcian and Aalenian forms, that the two are best kept separate. But I will leave him to discuss the taxonomy and variability of these later species such as *H. battalleri* (Dubar) (which he regards as a local subspecies of *H. meridionalis*).

THE TOARCIAN TAKEOVER

Looking at the genus *Homoeorhynchia* in general there is no doubt that, apart from the rare and local forms mentioned above, *H. acuta* is the dominant species of the Pliensbachian. When one comes to the Toarcian it is *H. meridionalis* that takes over almost everywhere that rich brachiopod faunas are found outside the alpine belt.

What then were the palaeogeographical events that accompanied this change? I have elsewhere

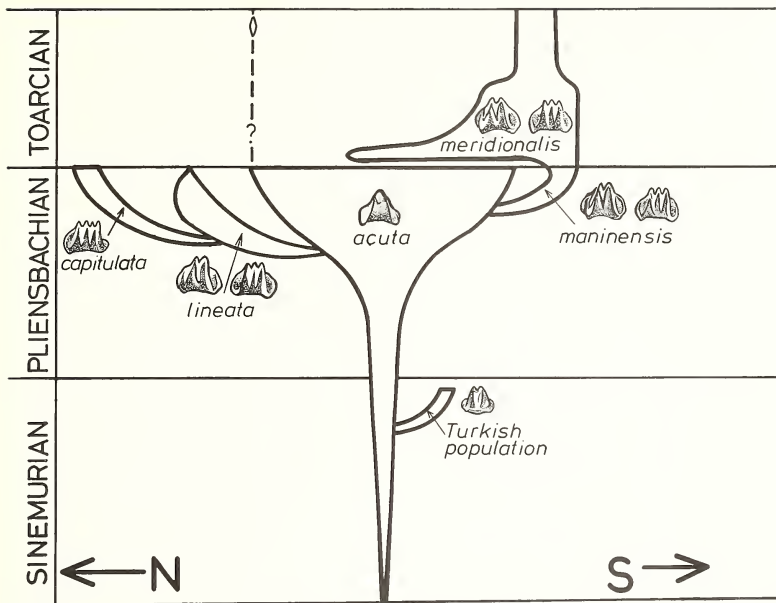


TEXT-FIG. 5. Variation in *Homoeorhynchia meridionalis*, Ham Hill Stone, Toarcian, Somerset. Symbols as in text-fig. 3.

suggested (Ager 1981) that the Toarcian transgression was one of the most important events of Mesozoic times. It was an episode of eustatic deepening on an almost world-wide scale with—for instance—the first Mesozoic flooding of the East African Seaway. Hallam (1981) has shown that episodic deepening of the sea was the leitmotif of early Jurassic history and that there was a major pulse in early Toarcian times. In Europe it was a time when shallow water carbonates and ironstones were generally replaced by black shale deposition and there was a general replacement of benthonic by pelagic faunas. Hallam (1967, 1972) has drawn attention to the 'profound turnover of the invertebrate fauna' with widespread extinctions of benthonic forms at this level.

It has earlier been hinted that marginal populations of *H. acuta* times might have been adapted to slightly deeper facies. It would therefore be logical to deduce that the spread of deeper water conditions favoured the marginal populations and enabled them to take over the regions previously occupied by the ancestral group. That it may not be as simple as that is suggested by the fact that the multicostate condition is 'normal' for Mesozoic rhynchonellids whereas the unicostate condition is decidedly 'abnormal'. It may therefore be that it was only rather special circumstances in the Pliensbachian that favoured *H. acuta* and with the return of 'normality' in the Toarcian (at least in its carbonate facies) the more usual and conservative *H. meridionalis* type reasserted itself. Clearly, however, there were advantages in the cynocephalous form since it was tried several times in the evolution of the Rhynchonellida, both in the Palaeozoic and in the Mesozoic (e.g. in *Pugnax*, *Ladogia*, and *Rhynchonella* s.s.).

The advantages of the *meridionalis* morphology are not easy to determine. It is conventional to associate multicostate shells with a sieving function when feeding (as originally suggested by Schmidt 1937). However, there seems to be no consistency in the lithologies associated with the contrasting morphological types. *H. acuta* occurs in calcarenitic type matrices (particularly ferruginous oolites) whereas its later homoeomorph *Rhynchonella loxiae* (Fischer de Waldheim)—the original type species—occurs in glauconitic clays. *H. cynocephala* occurs in sands and oolites, *H. lineata* in sideritic mudstones, and *H. meridionalis* is found in everything from lutitic calcareous marls to calcarenites (especially non-ferruginous oolites). What is more, in formations such as the Junction Bed on the Dorset coast, *H. acuta* is closely associated in the same thin bed with multicostate rhynchonellids such as *Quadratrhyndia crassimedia* (Buckman) and *Prionorhynchia serrata* (Sowerby).



TEXT-FIG. 6. Diagram showing the various populations of *Homoeorhynchia acuta* and its relations in the lower Jurassic and the suggested replacement of that species by *H. meridionalis* in the Toarcian.

CONCLUSIONS

Homoeorhynchia is the only genus I know, of literally hundreds of genera of Mesozoic Brachio-poda, that appears to show good evidence of allopatric speciation. There may be hints of it elsewhere, for example in *Aulacothyrus* (mentioned above), in *Plesiothyris verneuili* (Eudes-Deslongchamps), which may be the very local ancestor of the mid-Jurassic biplicate terebratulids, and in the southern *Quadratrhyrnychia* variants of *Tetrarhynchia*, but the general picture seems to fit in with the Gouldian doctrine of 'hardly ever'. Certainly there is no evidence in the group as a whole of phyletic gradualism happening throughout a species at any one moment in time. Species A never changes into species B everywhere simultaneously and gradually.

The pattern in any one place at any one time is of sudden replacement of one species by another. Thus, for example, in the lower Lias section at Hock Cliff (Gloucestershire), where the environment seems to be stable and the rest of the fauna (such as *Gryphaea arcuata*) is uniform, the rhynchonellid *Piarorhynchia juvenis* (Quenstedt) is replaced, from one bed to the next, by the closely related *Cuneirhynchia dalmasi* (Dumortier). The genera may be artificial but the distinctiveness of the two related species is indisputable and there are no gradations between them.

So far as *H. acuta* is concerned, there seem to have been several 'attempts' to return to the more conservative multicostate form. These 'attempts' were scattered both in time and space. Finally, however, populations appeared on the southern margin of the species' range, perhaps in slightly

deeper water, which then replaced the parent species with the coming of the Toarcian transgression (text-fig. 6). As Dodson and Hallam have pointed out (1977): 'a gradient can give rise to allopatric speciation and . . . it is not necessary to invoke the creation of geographic barriers or sharp environmental changes'.

In these marginal populations, phyletic gradualism must have taken place, though it cannot be recognized in the strata at present. What is seen more generally, with the degree of resolution that is available to us, is the punctuated equilibrium situation in the sudden take-over by *H. meridionalis* of most of the regime previously occupied by *H. acuta*.

In conclusion it may be said that phyletic gradualism must occur, but when it does, then paradoxically, it must happen very quickly.

Acknowledgements. I should like to express my thanks to Professor Akira Morishita and the University of Nagoya, Japan, where I was a guest when this paper was being written. I am grateful for discussions with Dr. J. Ferguson, Dr. M. J. Clutson, Dr. P. Styles, and Professor F. T. Banner and for guidance in the field to Dr. M. Siblik and the late Professor M. Gouvernet. Mr. J. U. Edwards kindly drew the diagrams and Mrs. V. M. Jenkins typed the manuscript.

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TOOTH REPLACEMENT IN A NEW GENUS OF PROCOLOPHONID FROM THE EARLY TRIASSIC OF CHINA

by LI JIN LING

ABSTRACT. A new genus of procolophonid, *Eumetabolodon*, from the lower Triassic of Inner Mongolia, China, is described; *E. bathycephalus* (sp. nov.) is the type-species of the new genus and *E. dongshengensis* (sp. nov.) is also referred to that genus. *Eumetabolodon* is characterized by its very deep skull, large orbit, and by the posterior position of the articulation for the lower jaw. The dental morphology, the tooth wear, and the evidence of tooth replacement in this animal are also described in detail. It is suggested that the animal replaced its teeth during growth, for it seems that the conical post-canine teeth of young individuals are replaced by transversely broad, bicuspid teeth, which are themselves replaced in turn by the next generation of teeth. The replacement of individual teeth is discussed; the sequence and rate of replacement are still unknown.

Two previous papers have described procolophonids from China: a single skull from Yushe, Shanxi province, as the new genus *Neoprocolophon* (Young 1957), and three teeth from the lower Er-Ma-Ying Formation (lower Triassic) of Baode county, Shanxi province, as *Paoteodon* (Chow and Sun 1960). (Romer 1966 referred to the latter incorrectly as being of upper Triassic age.) The present paper is based upon a number of incomplete skulls which were collected by two field groups of the IVPP in 1977 and 1979 from the north-eastern part of the Shaan-Gan-Ning Basin, in the border region between Inner Mongolia and Shaanxi province. The distance between the two localities, Zhuengeerqi and Gucheng, is 17.5 km (text-fig. 1). Most of the fossils were found in the upper He-Shang-Gou (He-Shan-Kou in old use) Formation. Three other groups of tetrapods have previously been identified from the same formation: scaloposaurs, pseudosuchians, and labyrinthodonts (Sun 1980). A few procolophonids have also been discovered in the lower Er-Ma-Ying Formation, together with a large number of dicynodonts, some primitive thecodontians, and scaloposaurs.

Because the new specimens show clearly characters different from those of previously described genera, a new genus is erected in this paper. The name *Eumetabolodon* is proposed, from the Greek *εὐμετάβολος* (changeable) and *ὀδούς* (tooth), because there is evidence that it developed replacement teeth during its lifetime. The specimens are in the Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing.

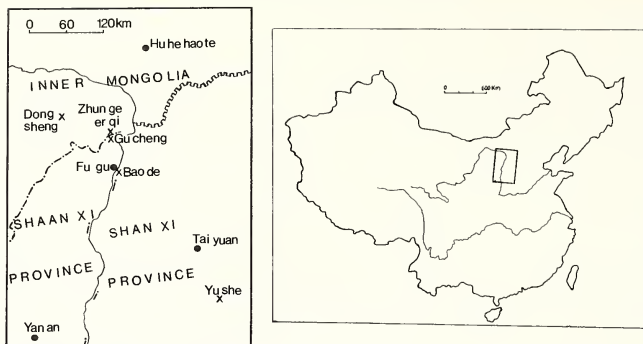
SYSTEMATIC PALAEONTOLOGY

Family PROCOLOPHONIDAE
Genus EUMETABOLODON nov.

Diagnosis. Skull generally triangular, relatively deep and broad posteriorly; orbit large, trapezoid; pineal foramen rounded, of medium size, located anterior to the posterior margin of the orbit, bordered anteriorly by the frontals; tabular and squamosal, quadratojugal and quadrate extend slightly obliquely backward; jaw articulation placed far posteriorly, just under the posterior rim of the skull table; otic notch distinct.

Eumetabolodon bathycephalus sp. nov.

Etymology. The species name is derived from the Greek *βαθός* (deep) and *κεφαλή* (head).



TEXT-FIG. 1. Localities at which procolophonids were found are shown by x in map on left, which is an enlargement of the rectangular area shown in map of China on right.

Diagnosis. Maxillary teeth separated by gaps between their bases, relatively short; may be longitudinally elongated in small animals, transversely widened and bicuspid in larger ones.

Holotype. V.6064, an almost complete skull and lower jaw.

Paratypes. Specimens (all skull material), as listed below.

Locality and Horizon. Zhuengeerqi county, Inner Mongolia, China; upper He-Shang-Gou Formation, T₁.

Description. The holotype is a well-preserved skull with lower jaw interlocked; both stapes are missing. Only the right quadrate, the rear of the right ramus of the lower jaw, and the snout are slightly broken. Thus the whole structure of the skull can be reconstructed with confidence (text-fig. 2).

Dorsal view. The posterior part of the skull is almost parallel-sided but, from a level midway along the orbits, the skull tapers anteriorly to a blunt snout. There is therefore, in dorsal view, a pronounced angulation in the skull profile, in which it is very different from the almost triangular skull of *Procolophon*, with its straight cheek region and postero-laterally directed quadratojugal bones. The large, irregular orbits occupy nearly half of the total skull length. The skull is high, and the orbits are therefore directed dorso-laterally.

Though the skull is well preserved, it is impossible to trace some of the sutures.

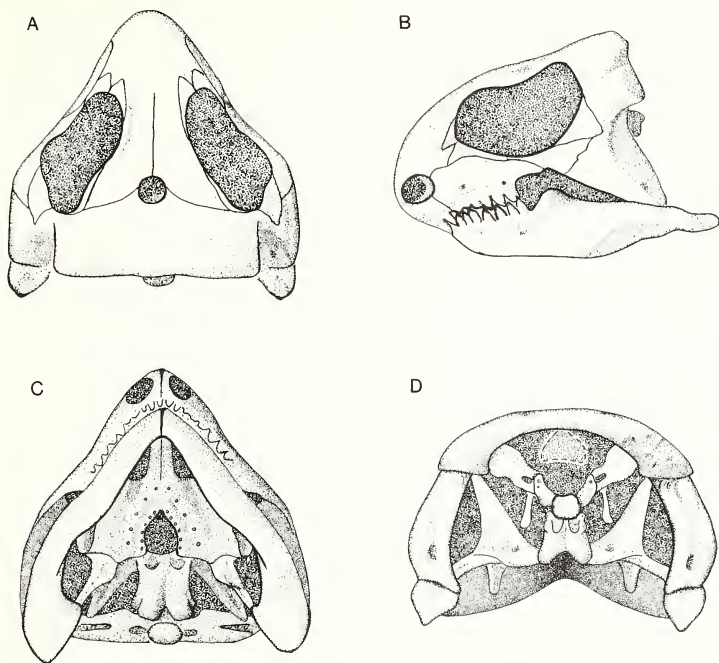
The nasals are badly damaged, only a small piece of the right nasal remaining. The lacrimals are, as usual, short and do not reach the external nares. The frontals are large and are unusual in that they, rather than the parietals, form the anterior border of the pineal foramen.

Side view. The jaws are closed in their natural position, the upper teeth being outside the lower teeth and interlocking with them. Only a few of the upper teeth are broken. This view clearly shows the great depth of the skull, both posteriorly and anteriorly; its maximum depth is 3.5 cm, nearly 70% of the skull length. The jaw articulation is placed very far posteriorly. The jaw symphysis shows a clear gap, which implies there was some mobility between the two rami of the lower jaw during life.

The external naris is large and elliptical. No trace of a septomaxilla could be found. The suture between the maxillae and the jugals is firm, not overlapping as in *Tichvinskia* (Ivachnenko 1973); this suggests that there was no mobility in *Eumetabolodon* at this position.

A longitudinal ridge separates the maxilla into two parts, the lower of which, a curved belt above the dentition, is directed ventro-medially. A noticeable foramen lies above the third maxillary tooth. Ivachnenko, who named this the anterior maxillary foramen, suggested that it transmitted an artery, a nerve, and perhaps also a vein. Another smaller foramen opens at a slightly more ventral level above the sixth maxillary tooth. It is also worth noting that, because of the deeper maxillae of *Eumetabolodon*, the foramen lies further from the tooth row than in *Tichvinskia*.

In having a very posteriorly placed jaw articulation, and consequently an unshortened lower jaw,



TEXT-FIG. 2. *Eumetabolodon bathycephalus* (gen. et sp. nov.), specimen V.6064, natural size. A, dorsal view; B, lateral view; C, ventral view; D, occipital view.

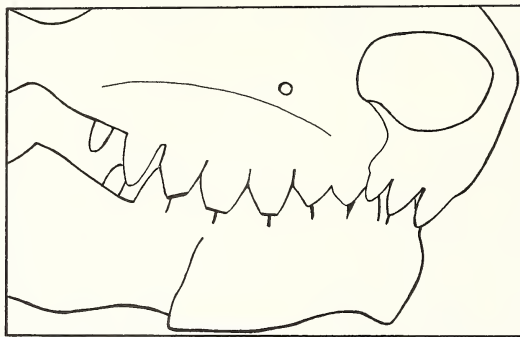
Eumetabolodon appears to be a primitive type of procolophonid. The lower jaw, which has a long retroarticular process, is therefore as long as the skull. The quadrate bears two condyles.

Because the teeth are tightly interlocked, it is difficult to study the details of the structure of the teeth, but several points can be noted. The upper and lower tooth rows are each 19–20 mm long. On the right side there are three premaxillary teeth and seven maxillary teeth, but on the left side there are two premaxillary teeth and six maxillary teeth. The premaxillary teeth are long and conical, and gradually diminish in size posteriorly. Behind the second premaxillary tooth on the left side there is a 1 mm gap, which is not seen in other specimens. The suggestion that the left tooth row is at a slightly earlier stage of development than the right is supported by the fact that its tooth row is also slightly shorter, with one maxillary tooth fewer. The last, seventh maxillary tooth on the right side is small and conical, unlike the larger, more anterior teeth. The last, sixth, maxillary tooth on the left side is large, and it seems unlikely that on this side the small seventh tooth had already been lost and would be replaced. It therefore seems more likely that it had not yet erupted.

The first and second maxillary teeth on both sides are so badly damaged that one can only say that they were small in size; their shape is unknown. The more posterior teeth increase noticeably in size and were apparently transversely widened. The posterior view of the sixth left maxillary tooth shows that it has two cusps, lingual and labial. The teeth are long (c. 2.5 mm) relative to the height of the skull. Their crowns are covered with clear brown enamel. In several, the cusps have worn away. The wear facets do not seem to show a similar oblique direction,

parallel in each tooth, as in *Hypsognathus* (Colbert 1946), but are irregular (text-fig. 3). The fact that the teeth are only slightly worn suggests that the specimen was a young individual. The dentitions of the two sides of the lower jaw are similar, each bearing eight teeth, of which the last is conical or blunt in shape.

Ventral view. The palate is of normal procolophonid structure, with large pterygoids surrounding a short, wide, heart-shaped interpterygoid vacuity as in *Procolophon*. There are two rows of small conical teeth, one row along the side of the interpterygoid vacuity and the other more lateral. The deep sockets on the pterygoids, which articulate with the parasphenoid, appear to face postero-dorsally rather than postero-medially as in *Procolophon* (Kemp 1974); this may be connected with the fact that the skull of *Eumetabolodon* is much deeper. The transverse palatal flange, formed by the pterygoid, almost touches the medial surface of the lower jaw. There can, therefore, have been little transverse movement of the latter.



TEXT-FIG. 3. *Eumetabolodon bathycephalus* (gen. et sp. nov.), specimen V.6064, $\times 4$. Lateral view to show dentition.

The quadrate ramus of the pterygoid extends horizontally and then twists gradually to suture with the quadrate as usual. Near where the pterygoid meets the parasphenoid, another long, strong spur of the pterygoid rises dorso-laterally to meet the squamosal. The suture between the ectopterygoid and the palatine, though hardly visible, is marked by a long, narrow palatonasal fenestra (Ivachnenko 1973). The vomers are damaged; no teeth can be seen on them.

The para-basisphenoid is very similar to that of *Procolophon*, described very carefully by Kemp (1974), so only a few differences need be mentioned here. The first is that the para-basisphenoid of *Eumetabolodon* extends postero-dorsally to meet the occipital condyle, which is at a higher level than the pterygoid; this makes a distinct angle between the palatal surface and the axis of the para-basisphenoid. Secondly, a very clear suture separates the parasphenoid from the basisphenoid; the former is 9 mm long, the latter 4 mm. The third point worthy of mention is that the contact between the basisphenoid does not rise as a delicate, vertical sheet to contact the anterior end of the prootic, as was described by Kemp (1974). No cultriform process can be seen.

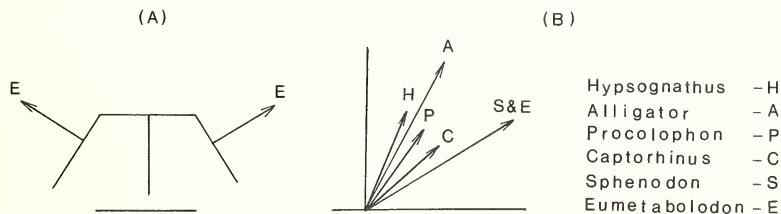
Posterior view. This shows clearly the great height of the skull. It is 15 mm from the upper margin of the occipital condyle to the top of the skull and a similar distance from the lower margin of the condyle to the surface of the quadrate condyle, so that the occipital condyle lies equidistant at the centre of the posterior surface. The basioccipital forms the whole of the condyle. It is small, rounded, and different from that of *Procolophon*, as there is no medial cleft and merely a low convexity on either side (Kemp 1974). The supraoccipital is a small triangular bone, displaced anteriorly. The exoccipitals, making up the lateral walls of the foramen magnum, resemble those of *Procolophon*. As mentioned by Watson (1914, p. 736) 'the bone extends outwards for a little distance with its upper part in contact with the posterior surface of the paraoccipital, from which bone it is separated below by the large, round foramen jugulare'. But in *Eumetabolodon* the dorsal part of the bone is penetrated by two foramina, a larger dorsal foramen and a smaller ventral foramen.

In *Procolophon* the opisthotic described by Kemp (1974) 'runs horizontally and somewhat posteriorly and slightly ventrally as a very well-developed process'. However, in *Eumetabolodon* it extends dorso-laterally to meet the tabular. The situation is more like that in *Nyctiphruretus*. The epipterygoids are very slender.

Discussion. The triangular skull, enlarged orbits, and few, apparently transversely widened teeth show that *Eumetabolodon* is a procolophonid. It is not difficult to distinguish *Eumetabolodon* from most other lower Triassic procolophonids, for it shows a number of unique features, notably the short high skull with large orbits and short snout, the anterior position of the pineal foramen so that it is partly bordered by the frontals, and the long lower jaw articulation near the posterior end of the skull. However, it also shows many resemblances to *Procolophon* itself and seems particularly close to *Koiloskiosaurus* (von Huene 1911). *Eumetabolodon* appears to be a smaller form than *Koiloskiosaurus*, though this difference must be treated with caution since we could be dealing with individuals of different ages. A more reliable difference lies in the skull proportions. The skull of *Eumetabolodon* is short and deep, whereas that of *Koiloskiosaurus* has an elongate snout and is more flattened; the skull of *Procolophon* is intermediate in these characters.

Such a change in skull height and width must cause a change in orientation of the orbits. Colbert (1946, p. 242) noticed 'this change in the direction of the orbits was the result primarily of transverse growth in the skull, from the primitive Permian and Lower Triassic procolophonids to the most specialized Upper Triassic genera. As the skull broadened, it flattened out, and with this flattening there was an accompanying change in the pointing of the orbits from a lateral to an almost vertical direction.'

The early representatives of this group, *Nyctiphruretus* (Efremov 1938) and *Owenetta* (Broom 1939), have flattened skulls. From the Permian to the early Triassic, the relative height of the skull increased. Colbert (1946, fig. 8) shows the direction of the orbits of a number of procolophonids and other reptiles in anterior or posterior view. The direction of the orbits of *Eumetabolodon* coincides with that of *Sphenodon*, which has a much narrower head (text-fig. 4). From the early to the late Triassic the procolophonid skull increased more rapidly in width than in height, so that the orbits became gradually more dorsally directed.



TEXT-FIG. 4. Diagrammatic cross-sections of reptilian skulls to show angles of the orbits. A, *Eumetabolodon*. The skull roof is shown by the upper horizontal line, and the arrow is drawn at right angles to the orbit. B, comparison of several reptiles (after Colbert 1946, with *Eumetabolodon* added).

In *Eumetabolodon* the distance between the posterior edge of the orbit and the posterior edge of skull is similar to that in *Procolophon* and *Koiloskiosaurus*. However, in *Eumetabolodon* the pineal foramen has moved anteriorly so that its posterior margin lies a little anterior to the posterior edge of the orbits, whereas it is level with that point in the other two genera.

Though Colbert (1946) suggested that the enlargement of the orbit into an orbito-temporal opening was connected with the shortening of the lower jaw and specialization of the dentition, *Eumetabolodon* has developed a very large orbito-temporal opening but retains a lower jaw of normal length.

The characteristics of its teeth are discussed below.

Eumetabolodon dongshengensis sp. nov.

Etymology. Dongsheng is the small town near to where the specimen was collected.

Diagnosis. Maxillary teeth closely spaced, with long conical crowns.

Holotype. V.6073, a small portion of skull, including right frontal, prefrontal, lacrimal, maxilla with seven teeth, and right ramus of lower jaw.

Locality and Horizon. This specimen is the only one which was not collected by field parties of the IVPP. It was found by Liu Shu ren in 1956 in the Shih-Tien-Feng Formation, which has since been subdivided into the Er-Ma-Ying, He-Shang-Gou, and Liu-Jia-Gou Formations. The locality is Wusilangou, Hantai valley, Dongsheng town, Inner Mongolia, only several dozen kilometres from Zhuengeerqi county, where the other fossils were discovered.

Description. The dorsal bones are in poor condition, so it is impossible to describe every element in detail.

The distance from the front edge of the orbit to the back margin of the external narial opening is only 6 mm, indicating that this is a small animal, much smaller than *E. bathycephalus* (V.6064), in which the corresponding distance is 13 mm (text-fig. 5).

There are seven teeth. Six of these are certainly implanted in the maxilla, but the first one is in the area where a thin layer of premaxilla overlies the ventral surface of the maxilla. The base of the tooth is nevertheless implanted in the maxilla, and it is therefore regarded as the first maxillary tooth.

All seven teeth are long and conical. They increase gradually in size from front to back until the sixth; the last one is a small, young tooth. At their bases they almost contact each other, only narrow gaps existing between the fifth, sixth, and seventh.

Discussion. Collected from a locality far from those of the remaining specimens of *Eumetabolodon* group 1 (see below for description and discussion), V.6073 has a similar deep skull but shows remarkable differences in its dentition. The cheek teeth are longer than those of other small individuals of *E. bathycephalus*, and are so closely spaced that their bases almost touch. They are also all conical, lacking the cusps and the longitudinal elongation of the base found in some of the cheek teeth of the other specimens. V.6073 may therefore be regarded as the holotype of a new species, *E. dongshengensis*. The distinction might even be generic but, in view of the inadequacy of the material, it seems preferable, at least for the present, to leave V.6073 within the genus *Eumetabolodon*.

THE DENTITION OF *EUMETABOLODON BATHYCEPHALUS*

The collection includes eighteen incomplete individuals. One specimen (V.6070) was collected in the Er-Ma-Ying Formation at Zhungeerqi, Inner Mongolia. The holotype (V.6064) also was collected at this locality but in the He-Shang-Gou Formation. These two specimens are comparatively well preserved. All the remaining specimens were collected in the He-Shang-Gou Formation, at Gucheng, Shaanxi Province, and are in rather poor condition. Some are seriously damaged, being represented by nothing more than a small piece of jaw-bone with several teeth; some, unfortunately, were broken again during mechanical preparation, for the bone is invariably very soft and embedded in hard red sandstone. The specimens are rather varied in size, tooth shape, and the nature of their occlusal surfaces. It is difficult to compare them in skull structure because of their incompleteness, but they can be divided into four groups, according to their size and to the characters of their maxillary teeth (see also Tables 1 and 2).

GROUP 1. The smallest specimens; the distance between the posterior border of the external naris and the front of the orbit is 7–8 mm. There are three to four premaxillary teeth, six maxillary teeth, and six teeth on the lower jaw. The maxillary teeth have only a single cusp, being conical; some of them are strong and laterally compressed. The teeth are only very slightly worn.

GROUP 2. Medium-sized specimens; the distance between the posterior border of the external naris and the front edge of the orbit is 9–17 mm. There are three to four premaxillary teeth, six to seven maxillary teeth, and eight teeth on the lower jaw. The first maxillary tooth has only a single cusp, but

the remainder have an inner and an outer cusp and are transversely broadened. Slight wear has produced shallow occlusal facets.

GROUP 3. Larger specimens; the distance between the posterior border of the external naris and the front edge of the orbit is 20–21 mm. There are three premaxillary teeth and six maxillary teeth; the lower dentition is unknown. All the maxillary teeth are transversely broadened, but wear has removed all the cusps except on the most posterior or replacing teeth.

GROUP 4. A single very large specimen, the distance between the posterior border of the external naris and the front edge of the orbit being 28 mm. There appear to be nine teeth in both upper and lower jaws, but prolonged wear has removed almost all trace of them except for the two most posterior teeth.

The specimens are now described and illustrated (text-figs. 5–30) in order of size.

GROUP 1

V.6168 (1). A broken snout interlocked with the right ramus of its lower jaw, and the separate, seriously damaged left ramus of the lower jaw (text-fig. 6).

All the premaxillary teeth are round in basal cross-section. Pm 1 and left Pm 2 have a horizontal occlusal surface, but right Pm 2 and Pm 3 seem to have oblique occlusal facets on their lingual sides. They may have been cone-like when still unworn. The maxillary teeth, which are stouter and stronger than those on the premaxilla, increase in size backwards along the jaw as far as M5. The shapes of the anterior four teeth are difficult to see, because they are interlocked with the lower jaw. The right M2 appears to have been lost accidentally, for a short portion of it is still ankylized to the jaw-bone. The left M3 is a conical tooth with a blunt tip. M5 and M6 are of equal length and both are conical; M5, though stouter than M6, is strikingly compressed.

Six dentary teeth are concealed by the upper dentition, in lingual view they are obviously larger than the maxillary teeth. Wide gaps exist between adjacent teeth.

V.6168 (2). A right ramus of lower jaw (text-fig. 7).

There are six teeth. Teeth one to five are the same in height but different in diameter at their bases; the fourth is the stoutest. The first four teeth are compressed and increase gradually in width posteriorly. The fifth, a single-cusped tooth, shows clearly a transversely widened basal portion. The sixth, a small conical tooth is almost in contact with the fifth, whereas obvious gaps exist between the other teeth.

V.6170. A damaged snout with the left ramus of the lower jaw (text-fig. 8).

This specimen is unusual in that there are four premaxillary teeth on the left side. There are six maxillary teeth on the right side and five on the left. Six damaged dentary teeth are attached to the lower jaw.

The premaxillary teeth are peg-like. They are different from those of *V.6168* in having a pointed tip and an occlusal surface on the lingual side. The maxillary teeth are short; they increase in size along the jaw from the M1 as far as the left M3 and right M4. Most of them have lost their tip, only the posterior three on the left are well preserved. The M3, the largest on the left side, has a longitudinally elongated base and a smooth occlusal surface facing ventro-lingually. The M4 and M5 have complete single tips and are slightly compressed.

The dentary teeth are stouter than the upper teeth. No cusps remain, but their bases exhibit longitudinally elongated cross-sections except the first and the last (text-fig. 9).

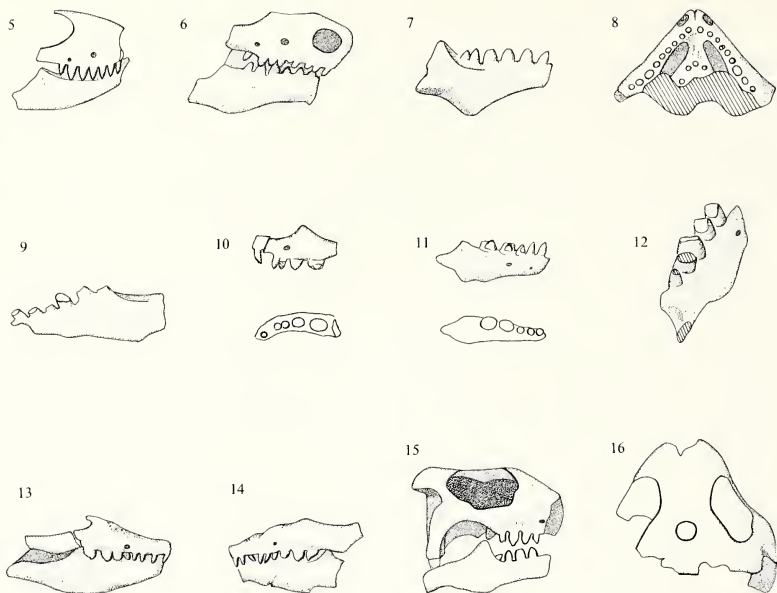
V.6172. A piece of the left side of the upper jaw (text-fig. 10) and the right side of the lower jaw (text-fig. 11).

The number of premaxillary teeth is unknown; only one has been left at the posterior end of the left premaxilla. Along the suture with the premaxilla, the maxilla has been pushed downwards a little. Associated with this, a small piece of the maxilla at the antero-ventral corner has been lost, causing a 1.5 mm gap between the last premaxillary tooth and the first maxillary tooth preserved; thus it is possible that the first maxillary tooth proper has been lost accidentally. Behind this gap, four teeth are borne on the maxilla. There are five dentary teeth. The premaxillary tooth, the second maxillary tooth, and the first two dentary teeth are all long, sharp, and peg-like. But the others are short, stout, laterally compressed, and increase in diameter posteriorly. Their crowns are incomplete but the pulp cavities, filled with matrix, show clearly that there was only a single cusp. At the bases of M4 and M5, there are clear sutures between the teeth and the bone; this suggests that the teeth have just erupted and have not yet fused to the jaw-bone.

GROUP 2

V.6171. A damaged snout with interlocked lower jaw (text-figs. 13, 14).

There are two premaxillary teeth on the right, three on the left, and six maxillary teeth on each side; the lower



TEXT-FIGS. 5-16. 5, *Eumetabolodon dongshengensis* (sp. nov.), specimen V.6073, right lateral view of snout; 6-16, *E. bathycephalus* (gen. et sp. nov.). 6, specimen V.6168 (1), right, lateral view of snout; 7, specimen V.6168 (2), right lateral view of lower jaw; 8, specimen V.6170, palatal view of snout; 9, specimen V.6170, left lateral view of lower jaw; 10, specimen V.6172, lateral and occlusal views of left upper jaw; 11, specimen V.6172, lateral and occlusal views of right lower jaw; 12, specimen V.6065, postero-ventro-lateral view of left upper jaw; 13, specimen V.6171, right lateral view of snout; 14, specimen V.6171, left lateral view of snout; 15, specimen V.6065, right lateral view of skull; 16, specimen V.6065, dorsal view of skull. Figs. 15 and 16, two-thirds natural size, remainder $\times 1\frac{1}{2}$.

teeth cannot be seen. M1 is long, thin, sharp, and conical. M2 has become transversely widened but longitudinally very narrow; the tip of the tooth on the left has a rounded profile in anterior view. It is difficult to establish the shape of M3 because it lies more medially. M4, M5, and M6 are stout.

V.6064. The holotype; see description above (p. 567).

V.6065. An incomplete skull and lower jaw (text-figs. 12, 15, 16).

As the anterior end of the skull and the symphyseal region of the lower jaw are missing, the dental formula is unknown. Only four maxillary teeth can be seen on the right side, and five on the left, and there are four dentary teeth on each side.

The maxillary teeth on the right are different from one another. The first tooth preserved, just under the anterior maxillary foramen, is short, transversely broad, and chisel-like. The main occlusal surface of the tooth is inclined steeply postero-ventrally, so that it makes a large angle with the flattened end. The second tooth preserved, also transversely broad, is larger than the first; it has an oblique occlusal surface and a horizontal end facet. The third, the biggest, is twice as high as the first; it has a wide base, an expanded middle part, and a narrow, contracted end. The fourth preserved is a small, thin bicuspid tooth, with the long axis of its cross-

section not parallel to that of the others; this suggests that, before it became a functional tooth, a rotation around the vertical axis would have taken place; which in turn, means that the tooth could not have been ankylized to the bone at the time of death. The characteristics of the four right maxillary teeth are similar to those of the left side.

On the right lower jaw ramus, the first and second teeth preserved are broken, but it is clear that they were transversely broad. The third preserved is thinner than the second and its cross-section seems to be rounder. A small and obtuse tooth had just erupted at the end of the tooth row; it is transversely widened but has only one rounded cusp.

The last four teeth in the lower jaw are recognizable on the left ramus. The broken cross-section of the first tooth preserved suggests that it was compressed. The second tooth preserved, the largest, has an oblique occlusal surface facing antero-labially; its lingual margin is much higher than the labial. The third of these teeth is damaged; only the basal part remains, showing a longitudinally elongated contour and the pulp cavity. It is possible that this is a new tooth, not yet ankylized. The last tooth is obviously smaller than its neighbour; it is transversely broad, with its long axis perpendicular to the margin of the jaw-bone. On both jaw rami the last tooth is too immature to show whether or not it would have been bicuspid.

V.6068. A small piece of right maxilla, right jugal, quadratojugal, quadrate, squamosal and right ramus of lower jaw (text-fig. 17).

Two teeth, one large, one small, are at the hind end of the upper jaw. The large one is very wide, with a horizontal occlusal surface. The small tooth has not been used, for it clearly shows two cusps.

There should have been seven teeth on the dentary, but the second is missing. They decrease in size from D1 to D3, then increase along the jaw until D6. D1-D4 are broken, D5 and D6 have an oblique occlusal surface facing labio-dorsally.

V.6069. A piece of left upper jaw and a piece of left lower jaw (text-fig. 18).

There are five upper teeth and three lower teeth, but the dental formula is unknown. The upper teeth are transversely widened, except the last which is irregular in shape. The first, fourth and fifth of those preserved have lost their crowns. The third, which is the largest, has a narrow end surface running labio-lingually, which separates an oblique anteriorly directed facet from a similar facet directed posteriorly. The second tooth preserved is obviously different from the third, having an almost horizontal end surface, but the postero-lingual part forms a curved depression. The dentary teeth are transversely broad; their lingual margins are higher than the labial, and their occlusal surfaces decline steeply.

V.6166 (1). An incomplete upper jaw and lower jaw of the left side (text-fig. 19).

Four premaxillary teeth and four maxillary teeth can be seen. The original number of teeth in the upper dentition is unknown, for the maxilla is broken posteriorly. There are very wide gaps on either side of M1. The last tooth M4 was large and transversely widened, but is broken too. There are two dentary teeth posterior to M4, which suggests that at least M5 had erupted and occupied the gap between D7 and D8. There are eight teeth in the lower jaw.

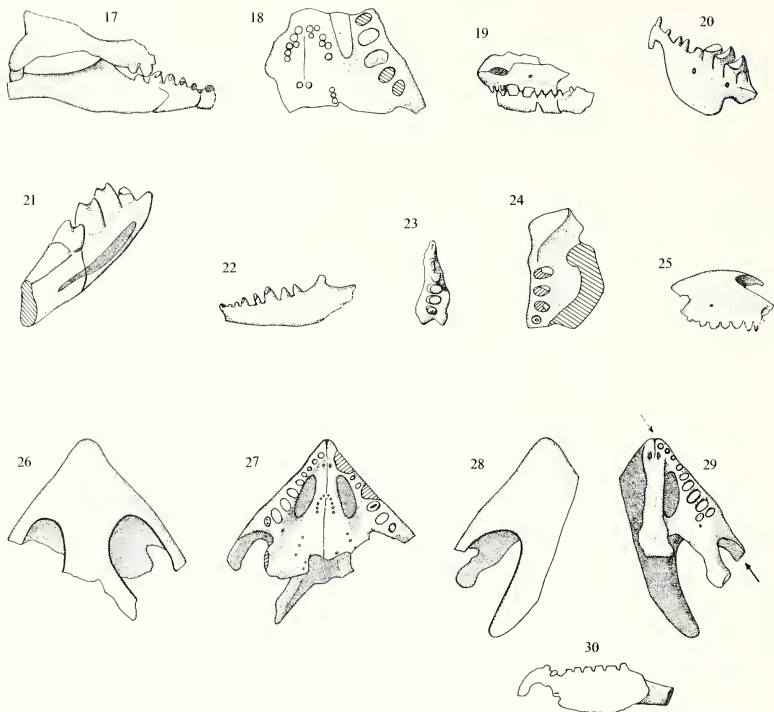
The premaxillary teeth are peg-like, decreasing in size from front to back. All had been used heavily, so obvious wear facets have formed on their lingual sides. A noticeable feature is that Pm1 and Pm2 are almost touching. D1-3 and D8 are conical; M1-4 and D4-7 are transversely widened and bicuspid. An interesting phenomenon is that there are very wide gaps between the teeth on the anterior part of the maxilla and those in the opposing region of the dentary, but neither new tooth buds nor broken tooth bases could be found in those gaps. The number of dentary teeth also proves that no teeth have been lost from the lower jaw. A possible explanation is that the gaps were formed by the growth of the jaw-bone and would be filled by the larger new teeth of the next generation, due to replace the older teeth.

V.6166 (2). The anterior part of a skull and a small section of the left lower jaw ramus (text-fig. 20).

On the right side there are three premaxillary teeth and six maxillary teeth. The number of dentary teeth is unknown. The teeth are strong and broad. Most of the premaxillary teeth are damaged, but the first is well preserved. They are widened in the direction of the tooth row. The lingual parts have been worn away and left a steep occlusal surface, so that the teeth are chisel-like. The maxillary teeth (except M1) are bicuspid, high, and very wide. M4 and M5 on the right show a very clear occlusal surface; on M4 this is curved and faces postero-ventrally, on M5 a transverse ridge separates the tooth crown into two parts, an anterior curved surface and a posterior surface. The last tooth on the right maxilla is small, round in the cross-section and has a blunt tip.

V.6169. A small piece of right lower jaw ramus (text-fig. 21).

The last four dentary teeth are present, increasing in size posteriorly as far as the penultimate. The anterior



TEXT-FIGS. 17-30. *Eumetabolodon bathycephalus* (gen. et sp. nov). 17, specimen V.6068, left lateral view; 18, specimen V.6069, palatal view; 19, specimen V.6166 (1), left lateral view of snout; 20, specimen V.6166 (2), postero-ventro-lateral view of right upper jaw; 21, specimen V.6169, postero-dorso-lateral view of lower jaw; 22, specimen V.6167, left lateral view of lower jaw; 23, specimen V.6173, palatal view of right upper jaw; 24, specimen V.6174, palatal view of right upper jaw; 25, specimen V.6175, lateral view of left upper jaw, 26, 27, specimen V.6066, snout in dorsal and palatal view; 28, 29, specimen V.6067 incomplete snout in dorsal and palatal view; 30, specimen V.6067, section through snout in plane of arrows shown in fig. 29. Figs. 18, 20, 21, and 24 $\times 1\frac{1}{2}$, remainder $\times 3$.

tooth has lost its tip; its width and length are equal on the cross-section of the basal portion. The second to fourth are bicuspid, with a sharp ridge connecting the two cusps; on both sides of the ridge there are deep and narrow concave facets, so that no occlusal surface could be seen.

V.6167. A left lower jaw ramus (text-fig. 22).

The first eight teeth are present, decreasing in size from D1 to D3, then increasing to D6 and decreasing again to D8. D1-D3 are conical, the others are transversely broad and bicuspid, but their length and width seems to be equal at the basal cross-section. The occlusal surfaces of D5 and D6 are at their tips; they are labially oblique, so that the lingual margins of the teeth are higher than the labial.

V.6173. A piece of right upper jaw (text-fig. 23).

The last four teeth are preserved, of which the second is the largest. They decrease in size anteriorly and posteriorly, and are transversely broad, but only the last is clearly bicuspid. On the second and third teeth the occlusal surfaces are basically horizontal, but small, shallow oblique facets exist on the front of the second tooth and the back of the third.

V.6174. A piece of right upper jaw (text-fig. 24).

The last four teeth are preserved; they increase in size from the first to the third but the fourth is the smallest. The anterior three are transversely broad, but unfortunately, their occlusal surfaces are damaged. The last tooth is rounded in its basal cross-section, but it has a blunt and slightly widened tip.

V.6175. An incomplete snout (text-fig. 25).

One premaxillary tooth and seven maxillary teeth are preserved on the left side. The premaxillary tooth is small and rounded in basal cross-section. The maxillary teeth increase in size from the M1 to M5, then decrease to M7. They are transversely broad and bicuspid; the distance between the two cusps depends upon tooth size (i.e. the wider the tooth, the longer the distance). Most of the teeth are damaged, but the curved occlusal surfaces facing postero-ventrally appear on the posterior side of the teeth from M4 to M7.

GROUP 3

V.6066. A damaged anterior part of a skull (text-figs. 26, 27).

There are three premaxillary teeth and six maxillary teeth on the right side. The premaxillary teeth are round in cross-section and decrease in size from front to back. The maxillary teeth increase in size from the first to the fifth; they have horizontal, flattened occlusal surfaces. The sixth, a small new tooth which had not yet ankylosed to the jaw-bone, clearly shows two cusps.

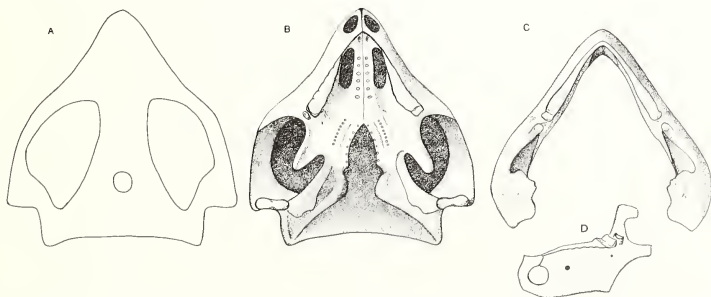
V.6067. A damaged anterior part of a skull (text-figs. 28–30).

This specimen is very similar to V.6066 in nearly every respect. However, the sixth maxillary tooth has been used and lost the tips of its cusps. Further, a new tooth has erupted from the inner side of the dentition between the fifth and sixth maxillary teeth; it is transversely broad and bicuspid, with a crown approximately the same height as the others. Finally, the third premaxillary tooth is very small, with only a short crown; a cross-sectional view shows that it inserts obliquely into the premaxilla.

GROUP 4

V.6070. An incomplete skull and lower jaw; some dorsal bones are missing, but traces of them show clearly the structure in dorsal view. The brain-case is missing (text-fig. 31).

All the teeth have been worn away on the premaxilla and the anterior part of the maxilla; no trace remains, so that it is impossible to count their exact number. Behind a point just under the anterior maxillary foramen, the



TEXT-FIG. 31. *Eunetabolodon bathycephalus* (gen. et sp. nov.), specimen V.6070, $\times \frac{1}{2}$. A, dorsal outline of skull; B, ventral view of skull; C, dorsal view of lower jaw; D, antero-ventro-lateral view of right upper jaw.

maxilla suddenly becomes wider; the teeth in this region have also been worn away except for the last two on both sides, but the number of the teeth can be counted because traces can be seen. On the right side there were evidently seven teeth. The last tooth but one is the widest. The last one is small, bicuspid, and lies parallel to the others. The condition in the lower jaw is the same as in the upper jaw; only two teeth remain at the posterior end. The ventral part of the left maxilla forms a longitudinal curved surface. It is depressed in the middle, but a little raised on the lingual and labial sides. On the right side of the upper jaw the lingual ridge has been lost so that the wearing surfaces occur ventro-lingually. The wear facets on both sides are remarkably asymmetrical. These toothless margins of the jaws were doubtless used to crush the animal's food (text-fig. 26).

Discussion. One species or two? It is clear from the above description that the specimens of the second, third, and fourth groups share certain similarities. They have transversely widened cheek teeth and a similar dental formula, the number of teeth being two to four in the premaxilla, six to seven in the maxilla (except V.6070, see below), and seven to eight in the dentary (see Table 1). The differences between them in skull size and the degree of tooth wear are also evident, and are probably due to differences in ages.

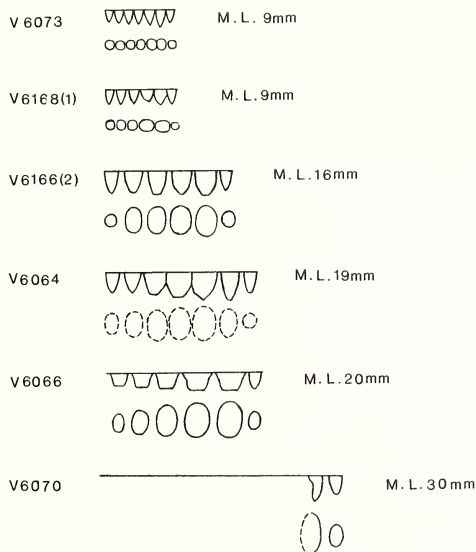
TABLE 1. Dimensions of the dentitions, and tooth formulae (all lengths in millimetres)

Specimen number	Distance between anterior margin of orbit and posterior margin of external naris	Length of premaxillary tooth row	Length of maxillary tooth row	Length of dentary tooth row	Average length of one maxillary tooth	Average length of each dentary tooth	Maximum height of maxillary tooth crown	Tooth formula		
								Pmx.	Mx.	Dent.
V.6168 (1)	8	4	9	10	1.5	1.7	2	3	6	6
V.6168 (2)	—	—	—	12	—	2.0	—	—	—	6
V.6170	8	3	9	13	1.5	2.1	1.7	3 (4)	6 (5)	6
V.6172	—	—	8	9	1.6	1.8	2.0	—	5	5
V.6171	—	4	10	—	1.6	—	1.7	2 (3)	6	—
V.6064 l.	13	5	14	20	2.3	2.5	3.0	2	6	8
V.6064 r.	13	5	19	20	2.7	2.5	3.0	3	7	8
V.6065	13	—	—	—	2.8	2.7	3.5	—	—	—
V.6068	—	—	—	24	—	3.4	3	—	—	7
V.6069	—	—	—	—	2.6	3.0	2.5	—	—	—
V.6166 (1)	14	—	—	22	3.0	2.8	2.5	4	5?	8
V.6166 (2)	15	8	16	—	2.7	—	3.5	3	6	—
V.6167	—	—	—	—	—	2.9	—	—	—	—
V.6169	—	—	—	24	—	3.0	—	—	—	8
V.6173	14	—	—	—	3.0	—	2.5	—	—	—
V.6174	—	—	—	—	2.2	—	2.0	—	—	—
V.6175	—	—	20	—	2.9	—	2.5	—	7	—
V.6066	20	7	20	—	3.3	—	1.8	3	6	—
V.6067	21	8	19	—	3.2	—	1.5	3	6 (7)	—
V.6070	28	8	30	32	—	—	—	—	≥ 9	—

The members of the first group, however, are small animals with fewer teeth. Their important characteristic is that their cheek teeth have but a single cusp. Some of the teeth are typically cone-shaped, some are expanded at the base, but no bicuspid teeth can be seen. For this interesting difference between the large and the small animals there are two possible explanations. The first is that they belong to different species, the smaller species with simple cheek teeth and the larger with bicuspid teeth. A similar phenomenon has been reported from South Africa; *Spondylolestes* (Broom 1937) is small with conical teeth and *Procolophon* is bigger with bicuspid teeth. The other explanation is that they all belong to the same species, which in early life had simple conical teeth, adapted to an insectivorous diet, but which later became herbivorous with transversely widened, bicuspid teeth. A similar ontogenetic change occurs in the living lizard *Varanus niloticus* (Edmund 1969).

The second interpretation seems preferable, for the following reasons. All twenty fossils (except V.6073 described here as *E. dongshengensis*) were discovered in one small area. There are fifteen individuals with transversely broad teeth, their sizes ranging from medium to very large; the smallest

of specimens with transversely broad, bicuspid teeth, V.6171, is slightly larger than the members of the first group. It would be very surprising if this group included none of the juveniles of one species but, by chance, several specimens of a second, smaller species. The second reason for viewing all of these specimens as members of one species is that tooth replacement could be clearly observed occasionally. For example, on the left maxilla of V.6067 a new bicuspid tooth has erupted which will



TEXT-FIG. 32. Diagrammatic representation of maxillary tooth rows of six specimens of *Eumetabolodon bathycephalus* in lateral and occlusal view. M.L., length of maxillary tooth row.

apparently replace an earlier, transversely broad tooth. The teeth of procolophonids, being either acrodont or protothecodont, fuse on to the dentigerous bone. Our fossils show clearly that the width of each tooth is almost equal to that of the jaw-bone at any developing stage. As the skull increased in size, the jaw-bone became stronger and the teeth became wider, especially behind the level of the anterior maxillary foramen on the upper jaw and the corresponding position on the lower jaw. It is reasonable to suggest that, in order to adopt a different habit of life and obtain enough food, a conical cheek tooth would be replaced by a transversely widened one as the animal grew.

It is worthy of note that there is an argument against this suggestion. For, lacking direct evidence of a conical tooth being replaced by a bicuspid tooth, V.6171 can be treated as the only juvenile of *E. bathycephalus* instead of as a representative of an intermediate type. In that case, the specimens in the first group (V.6168, V.6170, V.6172) would belong to another species, which remained small throughout life, bore single-cusped teeth, and shared the same habitat with *E. bathycephalus*. In order to resolve this problem, further fossil collection should be carried out. Meanwhile, however, all these specimens are provisionally referred to the species *E. bathycephalus*.

The process of replacement of an individual tooth. The evidence of tooth replacement in procolophonids was given by Ivachnenko (1974). Gow (1977) studied *Procolophon trigoniceps* and suggested a model of molar succession. It is clear that a replacing tooth germ developed initially from the dental lamina posterior and lingual to the tooth being replaced. The new tooth erupted from the jaw-bone and grew bigger and bigger until reaching the height of its predecessor. At this stage no pit or groove could be detected from the surface of the bone, as shown in *Ericiolacerta* (Crompton 1962). The actual replacement of an old tooth by a new one has never been seen, which suggests that the process of tooth replacement must have taken place very quickly. It is unlikely that an old tooth was shed, and that a new one then took its place. The present study does not confirm Gow's suggestion that teeth were lost at the front of the maxilla and dentary and that new ones were added at the rear of the tooth row.

The sequence of tooth replacement. The tooth shape of all of the specimens is shown diagrammatically in Table 2. Because of the incompleteness of the fossils, it is difficult to determine the exact sequence of their replacement, but the replacement tendency reflected by different groups seems to be more reliable.

In discussing *Contritosaurus simus* Ivachnenko (1974) stated: 'In connection with the appreciable differentiation of the teeth, replacement is occasionally observed only on the front teeth of the maxillary and the dentary. Replacement is hardly ever observed in the rear "quasicheek" teeth.' But the situation seems to be more complicated in another specimen. For example, it can be seen in *Phaanthosaurus ignatjevi* (Ivachnenko, 1974, fig. 1) that a new tooth has erupted behind and labial to the eighth dentary tooth (itself not preserved). Our fossils provide further evidence of tooth replacement, and suggest that it occurs not only in the front of the maxilla and dentary, but also at the rear of the maxillary tooth row (as in V.6067).

From Table 2 it can be seen that, at an early stage, the conical teeth on the maxilla and dentary appear to be replaced by another generation of single-cusped teeth, which are stronger and have a longitudinal elongated basal portion. This took place first in the maxillary teeth 3-5 and their counterparts in the dentary.

When the animals reached medium size, most of the cheek teeth had been replaced by transversely broad bicuspid teeth. This change seems to start in the second maxillary tooth. The first is often damaged but in a few instances is still preserved as a small conical tooth; at a later stage it would be replaced by a small widened tooth. Table 2 also shows that the biggest cheek teeth often appear at the fifth and sixth maxillary tooth positions, anterior to a small tooth. In some cases the fourth maxillary tooth is the biggest tooth on the upper jaw, there being two smaller teeth behind it.

At present there is not enough information about the exact sequence and rate of tooth replacement. Reptiles grow throughout life; but V.6070, a very old animal, which had worn away the teeth on most of its jaw, demonstrates that tooth replacement appears to cease after a certain growth stage is reached. No further teeth were produced and the animal probably crushed its food with the margin of its jaw-bone.

A characteristic of V.6070 worthy of mention is its large number of maxillary teeth. That might have been produced by adding new teeth to the back end of the jaws: the older the animal, the higher the tooth count. Another possibility is that the dental formula evolved a little with time; V.6070 is the only good specimen obtained from the bottom of the Er-Ma-Ying Formation which, though also lower Triassic in age, lies several dozen metres above the layer of the He-Shang-Gou Formation in which the other *Eumetabolodon* were found.

Tooth wear. The fossils clearly show regular correlation between the height of the teeth, the direction of the occlusal surfaces, and the age of the animals. When the animals were young, the crowns of the teeth were short, and generally the occlusal surfaces were not evident. When the animals reached medium size, their teeth attained maximum height (see Table 1 and text-fig. 32), but the occlusal surfaces seem to be irregular. In some cases, curved occluding facets appear on the posterior side of the upper teeth and the anterior side of the lower teeth (as in V.6065, V.6175). In other cases, occlusal facets lie obliquely at the end of the teeth. They face ventro-lingually on the upper teeth and dorso-labially on the lower teeth. At this stage the formation of occluding surfaces depends

TABLE 2

	Left ramus of upper jaw												Right ramus of upper jaw															
	Mx								Pmx				Pmx				Mx											
	9	8	7	6	5	4	3	2	1	4	3	2	1	1	2	3	4	1	2	3	4	5	6	7	8	9		
V.6073																		▲	▲	▲	▲	▲	▲	▲	▲			
V.6168 (1)							▲	△	▲		▲	▲	▲	▲	▲	▲		▲	△	●	●	●	▲					
V.6170					▲	▲	●	△	△	▲	▲	▲	▲	▲	▲	△		△	△	△	●	▲	▲					
V.6172					●	●	▲	▲			▲																	
V.6171				■	■	■	■	■	▲		▲	▲	▲	▲	▲			▲	■	■	■	■	■	■				
V.6064				■	■	■	■	□	□			▲	▲	▲	▲	▲		□	□	■	■	■	■	◆				
V.6065				◆	□	■	■	■													■	■	■	■				
V.6069				□	□	■	■	□																				
V.6166 (1)						□	■	■	□	▲	▲	▲	▲															
V.6166 (2)					□	□	■	■	▲		▲	▲	▲	▲	▲	▲		△	□	■	■	■	■	◆				
V.6174																				□	□	□	◆					
V.6173																				□	■	■	■	■				
V.6175				■	■	■	■	■	□		▲																	
V.6068																						■	■					
V.6066				□	□	□								▲	▲	▲		?	■	■	■	■	■					
V.6067				■	■	■	■	■	■		▲	▲	▲															
V.6070	■	■																						■	■			

	Left ramus of lower jaw												Right ramus of lower jaw																	
				9	8	7	6	5	4	3	2	1	1	2	3	4	5	6	7	8	9									
V.6168 (1)													▲	▲	▲	●	●	●												
V.6168 (2)													▲	▲	●	●	●	▲												
V.6170							△	△	●	●	●	△																		
V.6172													▲	▲	●	●	●													
V.6064				◆	■	■	■	■	▲	▲	▲	▲	▲	▲	■	■	■	■	▲											
V.6065				◆	□	■	□								■	□	■	◆												
V.6068													△	△	△	□	■	■	■											
V.6069				□	□	□																								
V.6166 (1)				△	■	■	■	■	▲	▲	▲																			
V.6167				■	■	■	■	■	△	△	△																			
V.6169																□	■	■	■											
V.6070				■	■																									

▲ Conical tooth.

● Enlarged and longitudinally extended tooth.

■ Transversely broad tooth.

◆ Small blunt tooth.

△ ○ □ Broken teeth.

▲ ● ■ The biggest teeth.

■ Replacing teeth.

| The end of premaxillary, maxillary, or dentary tooth row.

on the relationship of adjacent upper and lower teeth. At the beginning, because they had two cusps and a very narrow crest, the teeth could not make stable contact with each other at their tips. The posterior surface of the distal part of the upper teeth often contacted the anterior surface of the distal part of the lower teeth. As mentioned above, the two rami of the lower jaw were only loosely connected at the symphysis; this makes complex movement of the lower jaw possible and could thus result in a variety of shapes and directions of the occluding surfaces.

In large animals, represented by V.6066 and V.6067, the teeth have lost their tips and have flattened occlusal surfaces. This suggests that the animals needed a great deal of food and used their teeth heavily. At this stage tooth replacement continued; but, as any new tooth would have been worn down on reaching the height of the old ones, it could not be recognized after migrating into its position.

The last stage of tooth wear is clearly shown in V.6070. The wear surfaces are on the jaw-bone, and only two teeth remain at the posterior end of the row. This phenomenon appears also in some living reptiles. In *Uromastix* (as described by Robinson 1976) the anterior sectors of maxillae and dentaries are so heavily worn that the teeth have been abraded away entirely and the bony jaw margins are used in feeding. In V.6070 a special point worthy of notice (see above description) is that the occlusal surfaces are asymmetrical (text-fig. 27).

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CRINOID OSSICLES IN UPPER ORDOVICIAN BENTHIC MARINE ASSEMBLAGES FROM SNOWDONIA, NORTH WALES

by D. K. WRIGHT

ABSTRACT. Analyses of upper Ordovician (Caradoc) shelly faunas from Snowdonia, North Wales, reveal a remarkable diversity of crinoid columnals. So far, fifty-one columnal morphotypes have been recognized and these are listed, illustrated, and described. The morphotypes are categorized on the basis of earlier schemes of classification. The morphotype diversity implies that the original crinoid faunas were varied. Further applications of the columnal morphotype list include the potential recognition of morphotype combinations which originally comprised hetero- and xenomorphic columns and the possible use of the morphotypes in biostratigraphy.

BENTHIC palaeocommunity analysis is now an established sub-discipline within palaeontology. Although the holistic approach to community palaeoecology (Kauffman and Scott 1976) is accepted by many workers, the whole preserved fauna is rarely described (but see Jaanusson *et al.* 1979). In particular, taxa that are commonly found fragmented or dissociated are neglected, e.g. crinoids, bryozoans, cystoids, algae, and other groups, with the resultant loss of potentially valuable information.

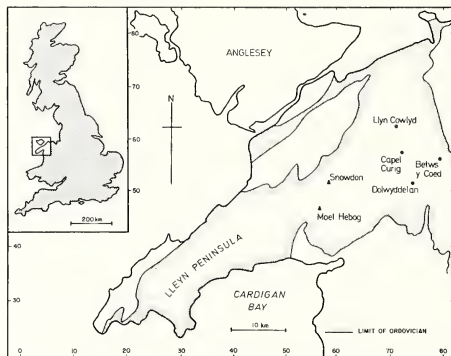
The present paper is based on a study of upper Ordovician (Caradoc) shelly faunas from the Glanrafon Beds and Snowdon Volcanic Group, and their equivalents. The faunas were collected from several areas within Snowdonia (text-figs. 1, 2). Analyses of the poorly preserved and tectonically distorted faunas, including dissociated and fragmented taxa, reveal relatively diverse assemblages (Wright 1979). Brachiopods are the dominant element of the faunas. Brachiopod associations, similar to those described by Williams, A. (1963, 1973) and Pickerill and Brenchley (1979) are recognized. Crinoids, though not abundant, are a widespread element of the faunas. This account presents an illustrated descriptive list of the columnals of this palaeoecologically neglected group, in addition to associated problems and applications of the list.

In the nineteenth century, the first systematic geological investigations of Snowdonia revealed 'encrinurites' within shelly assemblages from Snowdon, Glyder Fawr, Moel Hebog, the Llyn Ogwen-Llyn Idwal area and Carnedd Llywelyn (Sedgwick 1838, p. 679; 1841, pp. 548, 549; 1843, p. 219; 1847, p. 138; Ramsay 1866, pp. 85, 88, 126, 173, 215, 262, 273, 283-284). Later, more detailed work discovered further assemblages yielding 'encrinurites' and crinoid columnals from the Glanrafon Beds and Snowdon Volcanic Group of various areas within Snowdonia (Williams, H., 1927, p. 368; Williams, D., 1930, p. 206; Williams and Bulman 1931, p. 431; Shackleton 1959, pp. 233, 235, 241; Beavon 1960, p. 29; 1963, pp. 486, 487, 492, 508; Diggens and Romano 1968, p. 37; Romano and Diggens 1969, p. 603; Howells *et al.* 1978, pp. 67-70). Although earlier work indicates crinoids to be an important element of the Snowdonian benthic shelly assemblages, no detailed analyses of them have been undertaken. Figured specimens are deposited in the National Museum of Wales.

CRINOID COLUMNALS: *IN SITU* OR TRANSPORTED?

It is important to assess whether the fossil assemblages have been subjected to significant lateral transport prior to burial. Both physical and biological criteria are employed in this context, but the Palaeozoic palaeoecologist places greater reliance on such physical criteria as the fabric of the shelly

horizons, opposing valve ratios, articulation ratios, degree of abrasion and fragmentation, the enclosing lithology, and associated sedimentary structures (Pickerill and Brenchley 1979; Wright 1979). In the case of crinoid ossicles, physical criteria may not always prove to be so diagnostic, because low velocity currents, which would not affect the macrofauna, could transport such small biogenic particles. Most investigations reveal transportation only exerts a minor influence upon recent and fossil shelly assemblages (Ausich *et al.* 1979; Bretsky 1970b; Cadee 1968; Calef and Hancock 1968; Lane 1973; MacDonald 1976; Peterson 1976; Warne 1971; Warne *et al.* 1976). These investigations further suggest that whereas between-habitat transport is negligible, within-habitat small-scale transport is very likely. However, such studies usually are restricted to shelled macrofauna (in particular, brachiopods and bivalves), and have not included taxa which may disarticulate or fragment into many component parts.



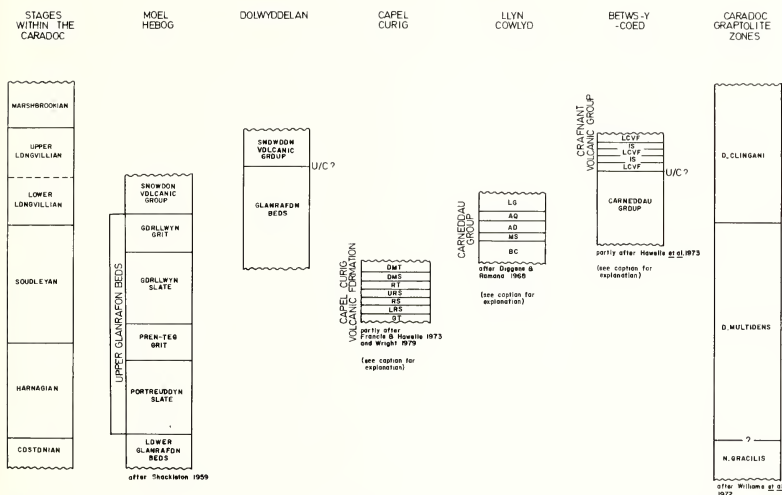
TEXT-FIG. 1. Regional setting of the study areas in Snowdonia.

With respect to crinoid ossicles, their open stereom meshwork (Marcurda *et al.* 1978) and low specific gravity, together with entrapped gases from organic decay (Cain 1968), makes them very light and thus susceptible to transport. Ossicles may undergo transient suspension transport (Schwarzacher 1963; Ruhmann 1971; Herm 1972; Seilacher 1973) which would not produce abrasion. Thus it is occasionally difficult to differentiate indigenous from exotic ossicles purely on surface condition.

Recent studies show that post-mortem crinoid disarticulation starts at the arm tips and proceeds towards the calyx (Meyer 1971; Brower 1973; Liddell 1975). Examples from the fossil record confirm such a sequence of disarticulation (Brower and Veinus 1974). This process is accelerated by persistent wave and current activity (Anderson 1968; Brower and Veinus 1974; Liddell 1975; Muller 1979). The rate of sedimentation is a critical factor governing crinoid preservation. Rapid sedimentation ensures the preservation of complete crinoids and arms (Liddell 1975; Brower and Veinus 1978), whereas crinoids often become entirely disarticulated in areas of reduced sedimentation, even when current velocities are low (Lane and Matthews 1965; Anderson 1968; Brower 1973; Brower and Veinus 1978). Transport of crinoid debris is likely in those areas with reduced sedimentation, although probably only within-habitat transport occurs when low rates of sediment deposition are associated with low velocity currents.

Biological and physical criteria show that most crinoid remains within the Snowdonian assemblages are essentially *in situ*. Here, *in situ* implies little or no significant lateral transport of the crinoid material from their living sites, rather than the crinoids being still attached. Crinoid arms

(Pl. 65, fig. 3) from the Portreuddyn Slate of the Moel Hebog district (text-figs. 1, 2), several complete crinoids associated with complete detached arms and twisted pluricolumnals (Pl. 65, figs. 1, 2, 5) from the Gorrllwyn Slate of the same district (text-fig. 2), together with rare crinoid crowns (Pl. 65, fig. 4) from the Glanrafon Beds at Dolwyddelan (text-figs. 1, 2), are unequivocally *in situ*. Transitory pulses of rapid sedimentation probably effected their preservation.



TEXT-FIG. 2. Stratigraphy for the study areas within Snowdonia. *Capel Curig area*: GT—Garth Tuff; LRS—Lower Racks Sandstone; RS—Racks Siltstone; URS—Upper Racks Sandstone; RT—Racks Tuff; DMS—Dyffryn Mymbyr Siltstone; DMT—Dyffryn Mymbyr Tuff. *Llyn Cowlyd area*: BC—Bwlch Cowlyd Formation; MS—Multiplicata Sandstone; AQ—Adwyn Owen Beds; AG—Arkosc Quartzite; LG—Llethr Gwyn Sandstones. *Betws-y-Coed area*: IS—Intercalated sediments; LCVF—Lower Crafnant Volcanic Formation.

The Portreuddyn Slate fauna is recovered from lenticular shelly concentrations displaying random orientations of the disarticulated brachiopod valves, within a fine-grained siltstone (Wright 1979). The two commonest components of the fauna are aegiomenine (*Sericoides*) and dalmanellid (*Dalmanella* and *Omiella*) brachiopods. Almost 50% of these genera are still articulated and disarticulated opposing valve ratios approach unity. As the valves of *Sericoides* probably disarticulated very easily (Bergström 1968), relatively low velocity currents could induce large-scale disarticulation, with consequent unequal valve dispersion resulting from their relative thinness and differing hydrodynamic properties. For *Sericoides*, the relatively high degree of articulation, opposing valve ratios approaching unity and unabraded, unfragmented valves all suggest very little current activity and thus insignificant lateral transport. It is likely the fauna accumulated relatively quickly within sea floor sediment traps. These traps then became rapidly buried. The enclosing siltstone displays parallel laminations of variable thickness (usually less than 1 cm), with some slightly coarser grained laminae. No bioturbation is noted. Such laminations imply slow, uniform sedimentation in a low energy environment, the slightly coarser material being deposited from suspension in slowly moving waters (Harms and Fahnestock 1965). Therefore it is unlikely that this

fauna has suffered any significant lateral transport, and thus can be regarded as being essentially *in situ*.

Entire crinoids and detached crinoid arms from the Gorllwyn Slate similarly indicate an *in situ* assemblage, as do associated unabraded, unfragmented ramose bryozoa and pluricolumnals. Thin (5–10 cm) fining-upwards sequences are noted within the enclosing siltstone, suggesting some level of fluctuating current activity and clastic input. Slight down-loading at certain horizons implies relatively rapid sedimentation. However, the palaeontological evidence seems to discount significant lateral transport of this assemblage.

Faunas from the Glanrafon Beds at Dolwyddelan have yielded crinoid calyces with the arms missing. The commonest brachiopods, e.g. sowerbyellids, dalmanellids (*Dalmanella* and *Howellites*), and plaesiomyids (*Dinorthis*), all possess disarticulated opposing valve ratios approaching unity. The valves themselves are unfragmented and unabraded. Such facts imply the assemblage has not undergone extensive lateral transportation, but minor current activity may be inferred from the armless calyces. The commonest brachiopods have less than 33% of their valves still articulated and most of the small disarticulated valves are in the hydrodynamically stable convex-up position. However, associated pluricolumnals with abundant cirrals and pinnates seemingly suggests any current activity present did not induce widespread sorting of the faunal components. The armless calyces could be explained by *in situ*, post-mortem disarticulation of the arms over a period of days on a quiet sea bed (Meyer 1971; Liddell 1975), the calyces then being buried and preserved by an influx of sediment. It is feasible that the abundant pinnates accompanying the calyces represent the disarticulated arms.

Shelly assemblages from the Crafnant Volcanic Group of the Betws-y-Coed district (text-figs. 1, 2) provide further examples of what are considered to be *in situ* accumulations. Collapsed diploporite cystoid thecae connote little significant lateral transport, although it is not known whether crinoids and cystoids underwent similar post-mortem disarticulation. However, currents undoubtedly were operative. The disarticulated valves of associated large brachiopods (*Nicolella* and *Orthambonites*) are always convex-up, unfragmented, and unabraded. In contrast, the valves of the smaller, commoner brachiopods (*Skenidioides*, *Protozyga*, and *Sericoides*) are commonly fragmented, have low articulation ratios and disarticulated opposing valve ratios which occasionally depart markedly from unity. They are noted in both convex-up and concave-up orientations. The author believes the larger valves were unaffected by current activity and are *in situ*, whilst the smaller valves suffered some degree of within-habitat transport. The robust cystoids were relatively unaffected by the currents. No entire crinoids are noted in these assemblages, but a diverse assemblage of columnal morphotypes is present. Consequently, it appears likely that the post-mortem disarticulation rate of crinoids and cystoids differed.

The vast majority of shelly assemblages from Snowdonia only contain disarticulated crinoid ossicles. Physical criteria suggest that the assemblages have suffered only minor within-habitat transportation.

Irrefutable proof of transported crinoid material is surprisingly rare. Assemblages deposited under high energy regimes, e.g. from the *Multiplicata* Sandstone of the Llyn Cowlyd district and the Racks Sandstone at Capel Curig (text-figs. 1, 2) contain sparse crinoid material. Such absence is explained either by transportation away from the original depositional areas or that the original environments were inimical to crinoid colonization. Palaeoenvironmental interpretations enforce the latter proposal.

Re-examination of the shallow water sediments from locality 129 (SH 71445803) within the Upper Racks Sandstone at Capel Curig (text-figs. 1, 2) reveal microscopic, fragmentary, frequently abraded echinoderm (crinoid?) remains. The fauna and sediments from this locality are correlated with the slightly deeper water sediments and fauna from the Glanrafon Beds at locality 225 (SH 76125104), south-east of Dolwyddelan (text-figs. 1, 2). Crinoid material is common at the latter locality and is similarly preserved to that found at locality 129. Thus, in this case, crinoid debris apparently was transported onshore from an outer sublittoral environment, probably by onshore storm surge currents.

Previous treatment of crinoid columnals in faunal analyses

Crinoid columnals are accorded different types of treatment in faunal analyses. They are either apparently ignored (Bretsky *et al.* 1969; Hurst 1975*a, b*; Bretsky *et al.* 1977; Byers and Gavlin 1979) or only their presence is recorded (Bretsky 1969, 1970*a, b*; Bowen *et al.* 1974; Feldman 1980). Further levels of treatment are the quantification of columnals (Ziegler *et al.* 1968; Watkins 1978; Pickerill and Brenchley 1979) and the recognition of columnal morphotypes, which are sometimes quantified (Titus and Cameron 1976; Hurst 1979*a, b*). Arbitrary correction factors are used by some workers to estimate the relative numbers of crinoids represented by the columnals and these range from 5 to 300 columnals being equal to one crinoid (Watkins 1973; Thayer 1974; Berry *et al.* 1979; Wright 1979). However, such correction factors are sometimes regarded with scepticism, as the estimates '... defy reality' (W. I. Ausich, pers. comm.).

CRINOID COLUMNAL MORPHOTYPES

Analyses of the shelly assemblages revealed columnal diversity was not satisfactorily defined by the term 'crinoid columnals' (Wright 1979). It was necessary to devise a classification of the different columnal morphotypes. Each morphotype has been recognized within the Snowdonian shelly assemblages, in contrast to the morphotype lists of other workers (see Jeffords 1978, T928-T929). The basis for the categories employed in the list of morphotypes is taken from a classification proposed by Moore (1939), and later elaborated by Moore and Jeffords (1968) and Moore *et al.* (1968). Following Moore's classification, the morphotype categories of the following list are based on: (a) transverse outline of the articular facet; (b) transverse outline of the lumen; (c) features of the articular facet. Genus groups (text-fig. 3) and morphotypes are differentiated using these criteria,

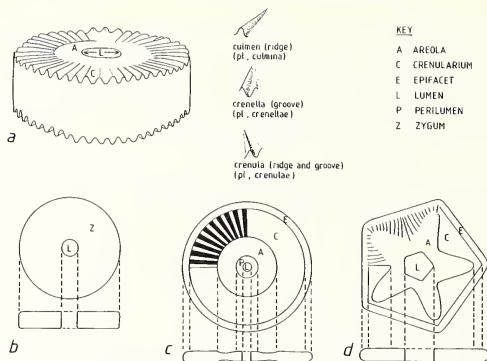
		TRANSVERSE SHAPE OF COLUMNAL				
		Cylo (C)	Penta (P)	Pentastella (PS)	Hexa (HEX)	Hemu (H)
						
TRANSVERSE SHAPE OF LUMEN	-cylo (c)					
	-tristella (ts)					
	-penta (p)					
	-pentastella (ps)					

TEXT-FIG. 3. Matrix illustrating the ten basic columnal genus groups found in the Snowdonian shelly assemblages. Shading denotes non-combination.

latinized binomina being applied to the genus groups (after Moore 1939), e.g. *Cyclocyclopa*. The 'prefix' (*Cyclo/cyclopa*) refers to the transverse shape of the articular facet, e.g.

Cyclo-	circular articular facet
Penta-	pentagonal articular facet
Hexa-	hexagonal articular facet
Pentastella-	stellate five-armed articular facet
Hemicyclo-	semi-circular articular facet

The 'suffix' (*Cyclo/cyclopa*) pertains to the transverse outline of the lumen and follows the same nominations. This method generates cumbersome genus group names, so a coding scheme is implemented (see next section). Features of the articular facet govern morphotype subdivision within each genus group.



TEXT-FIG. 4. Morphological features of crinoid columnals. *a*, oblique view of single columnal showing features of articulation surface. Single ridge (culmen) and groove (crenella) together form a crenula. *b-d*, facetal views and median longitudinal sections of different columnal morphotypes to show various morphological features.

All after Moore *et al.* 1968.

Of the three morphological features cited above, the transverse outline of the lumen is often regarded as being less variable than the other two features (Stukalina 1966), and thus possibly of greater importance when grouping the columnal morphotypes. The morphotypes in the following list are grouped primarily on the transverse outline of the articular facet. If, however, primary importance is attached instead to the transverse outline of the lumen and the morphotypes are grouped principally on the basis of this feature, a somewhat different system of groupings would result. Certain genus groups would become amalgamated, e.g. Cc with Pc; HEXc with HCc; Cp with Pp; Cps with Pps and PSpS. Depending on preservation, pluricolumnals can be assigned to a columnal morphotype. Intercolumnal articulation is sometimes visible (Pl. 65, fig. 7) and is usually symplectic (Ubahgs 1978a, T77).

EXPLANATION OF PLATE 65

Fig. 1. Twisted pluricolumnal associated with detached crinoid arms. Gorllwyn Slate, south of Moel Hebog. NMW 83. 14G. 1, $\times 3.1$.

Fig. 2. Complete crinoid. Bottom—stem; centre—poorly preserved theca; top—arm still attached to theca. Gorllwyn Slate, south of Moel Hebog. NMW 83. 14G. 2, $\times 3.4$.

Fig. 3. Detached crinoid arm. Portreuddyn Slate, south of Moel Hebog. NMW 83. 14G. 3, $\times 5.8$.

Fig. 4. *Balacrinus* sp. Theca. Glanrafon Beds, south-west of Dolwyddelan. NMW 83. 14G. 4, $\times 5.5$.

Fig. 5. Part of detached crinoid arm. Gorllwyn Slate, south of Moel Hebog. NMW 83. 14G. 5, $\times 5.5$.

Fig. 6. Pc 1 pluricolumnal showing nodals, three orders of internodals, and symplectic intercolumnal articulation. Glanrafon Beds, south-west of Dolwyddelan NMW 83. 14G. 6, $\times 8.1$.

Fig. 7. Curved pluricolumnal showing different orders of columnals (nodals? and internodals) and symplectic intercolumnal articulation. Glanrafon Beds, south-west of Dolwyddelan. NMW 83. 14G. 7, $\times 9.6$.



1



3



4



5



2



6



7

MORPHOTYPE LIST

The columnals described and illustrated in the following list are all represented in the Caradoc shelly faunas of Snowdonia. In all cases, the morphological terms applied to the columnals are defined by Moore (1978, T229-T242) and Moore *et al.* (1968, pp. 27-30), and are depicted in text-fig. 4. A coding scheme is implemented to replace the cumbersome genus group names and is as follows:

Cyclo-	C	-cyclopa	c
Pentagono-	P	-pentagonopa	p
Pentastella-	PS	-pentastellatopa	ps
Hexagono-	HEX	-tristellatopa	ts
Hemicyclo-	H		

Group CYCLICI. Circular columnals.

 Genus CYCLOCYCLOPA (Cc). Circular columnal with circular lumen.

Varieties



Cc 1

Variably sized lumen; smooth undifferentiated zygum.



Cc 1a

Variably sized lumen; zygum composed of wide crenularium; well-defined radial crenulae unbranched.



Cc 2

As for Cc 1a, except majority of culmina display centrifugal bifurcation.



Cc 3

Wide crenularium divisible into inner narrow section with simple culmina, and outer broader section where most culmina branch. Narrow areola occasionally developed.



Cc 4

Fulcral ridge extends across zygum and divides it into two smooth bifascial fields. Fulcral ridge may denote some degree of flexible articulation (synarthry) in crinoid stem.



Cc 5

Wide crenularium with spaced, thick culmina which occasionally bifurcate centrifugally and thin centripetally.



Cc 6

Wide areola; narrow peripheral crenularium of thin simple culmina; sides of columnal granulose.



Cc 7

Variably sized lumen; narrow band ('perilumen') of simple fine crenulae rims lumen; remainder of zygum smooth.



Cc 7a

As for Cc 7, except finely crenulate in transverse outline.



Cc 8

Depressed, narrow, radially ornamented perilumen.



Cc 9

Variably sized lumen; areola surrounded by narrow crenularium, in turn surrounded by smooth rim (?epifacet).



Cc 9a

As for Cc 9, except undulose in transverse outline.



Cc 10

Small lumen; three thin culmina traverse the otherwise smooth zygum.



Cc 11

Variably sized lumen; crenularium of thick crenulae surrounded by wide smooth rim (?epifacet).



Cc 12

Very small lumen; areola surrounded by peripheral crenularium of short, widely spaced crenulae.



Cc 13

Wide lumen; areola surrounded by peripheral crenularium of short, fine, closely packed crenulae.



Genus CYCLOTRISELLATOPIA (Cts). Circular columnal with tristellate-triangular lumen.



Cts 1

Tristellate lumen; smooth undifferentiated zygum.



Cts 2

Triangular lumen; zygum traversed by three culmina, each originating at one apex of triangular lumen.



Genus CYCLOPENTAGONOPA (Cp). Circular columnal with pentagonal-quinquelobate lumen.

Varieties



Cp 1

Narrow band of fine unbranched crenulae rims lumen (?perilumen).



Cp 2

Depressed narrow crenularium within groove rims lumen.



Cp 3

Smooth undifferentiated zygum.



Cp 4

Areola surrounded by narrow intermediate crenularium, in turn surrounded by smooth rim (?epifacet).



Cp 5

As for Cp 4, except finely crenulate in transverse profile.



Cp 6

Quinquelobate lumen.



Cp 7

Zygum traversed by paired culmina, each pair originating at an apex of pentagonal lumen and thence diverging centrifugally.



Cp 8

As for Cp 1, except undulose in transverse profile.



Genus CYCLOPENTASTELLATOPA (Cps). Circular columnal with pentastellate lumen.



Cps 1

Smooth undifferentiated zygum.



Cps 2

Wide crenularium; narrow areola may be developed.



Cps 3

Wide areola surrounded by narrow peripheral crenularium of fine unbranched crenulae.



Cps 4

Crenularium of broad, widely spaced culmina which widen centrifugally.

Group PENTAMERI. Pentagonal-quinquelobate columnals.



Genus PENTAGONOCYCLOPA (Pc). Pentagonal-quinquelobate columnal with circular lumen.



Pc 1

Complex zygum; areola subdivided into five discrete circular fields; a prominent culmen, slightly thickening centripetally, passes between adjacent fields, meeting columnal periphery approximately midway along each side of columnal; a crenularium partially surrounds each circular field, with simple culmina, separated by relatively broad crenellae, radially disposed at each apex of columnal but gradually becoming subparallel to one of the 'major' culmina.



Pc 2

Smooth undifferentiated zygum.



Pc 2a

As for Pc 2, except lower half of columnal is lobate, giving appearance of combined pentagonal and quinquelobate forms.



Pc 3

Zygum traversed by five fine culmina, which originate at lumen and terminate at each apex of columnal.



Pc 4

Five fine culmina originate at each apex of columnal, but do not extend to lumen.



Pc 5

Smooth undifferentiated zygum except for intermediate concentric groove.



Pc 6

Columnal possesses quinquelobate transverse profile; smooth undifferentiated zygum.



Genus PENTAGONOPENTAGONOPA (Pp). Pentagonal-quinquelobate columnal with pentagonal-quinquelobate lumen.

Varieties



Pp 1

Narrow band of fine unbranched crenulae rims lumen (?perilumen).



Pp 2

Pentagonal lumen is out of phase with respect to pentagonal shape of columnal in transverse profile; five fine culmina originate at each apex of lumen and meet columnal periphery approximately midway along each side of columnal.



Pp 3

Lumen shape in phase with pentagonal columnal shape; five fine culmina originate at each apex of lumen and terminate at each apex of columnal.



Pp 4

Quinquelobate columnal; very large quinquelobate lumen, bordered by slightly depressed groove possessing fine unbranched crenulae.



Pp 5

Narrow areola surrounded by narrow crenularium of short, fine, unbranched crenulae, in turn surrounded by smooth rim (?epifacet).



Genus PENTAGONOPENTASTELLATOPA (Pps). Pentagonal columnal with pentastellate lumen.



Pps 1

Apices of pentagonal columnal coincide with apices of lumen; smooth undifferentiated zygum.



Pps 2

Lumen orientation is rotated with respect to orientation in Pps 1.



Pps 3

Wide areola surrounded by narrow peripheral crenularium of fine unbranched crenulae.



Pps 4

As for Pps 2, except five fine culmina originate at apices of rotated lumen and traverse zygum; culmina meet columnal periphery approximately midway along each side of columnal.



Pps 5

As for Pps 3, except lumen orientation is rotated.

 Genus *PENTASTELLAPENTASTELLATOPA* (PSps) Pentastellate columnal with pentastellate lumen.

Varieties

PSps 1

Diagnosis as for genus; complex zygom smooth and undifferentiated.



Group VARII. This group contains genera that do not find a place in the other two groups.

 Genus *HEXAGONOCYCLOPA* (HEXc). Hexagonal columnal with circular lumen.

HEXc 1

Areola surrounded by narrow intermediate crenularium of fine unbranched crenulae, in turn surrounded by smooth rim (?epifacet).



HEXc 2

Smooth undifferentiated zygom.



 Genus *HEMICYCLOCYCLOPA* (HCc). 'Trough-shaped' columnal with circular lumen; very rare.

HCc 1

Zygom traversed by three fine culmina, each disposed at an approximate angle of 120 degrees to each other.



It is likely that some of the illustrated columnal morphotypes are meric (i.e. segmented), e.g. Cc 10, Cts 2, ?Cp 7, Pc 2, Pp 2, Pp 3, Pps 4, and HCc 1. Stukalina (1966; 1968, fig. 1) considers segmented columnals to be primitive and illustrates two types of segmentation found in pentagonal columnals (Stukalina 1966, p. 553, fig. 2). In the first, the suture lines of the individual segments run from the angles of the lumen, whilst in the second type, the suture lines are perpendicular to the walls of the lumen and the side of the columnal. The first type is represented in the Snowdonian columnals, e.g. Pp 3, and therefore it is possible that this morphotype is meric. Of the second type described by Stukalina, no morphotypes have, as yet, been found that are exactly identical. Certain morphotypes, however, show probable suture lines which are perpendicular to the sides of the columnal but which run from the angles of the pentagonal or pentastellate lumen, e.g. Pp 2, Pps 4. Thus, these morphotypes may also be meric.

The Asegmentata group of Stukalina (1966) comprises morphotypes with a circular lumen and a circular articular facet, but no morphotypes included within this group are segmented. The Cc genus group from the Snowdonian list would be placed within the Asegmentata group, but Cc 10 may be meric, contradicting Stukalina's diagnosis of the group.

Discussion. The list demonstrates the diversity of the columnal morphotypes (51) within the Caradocian shelly assemblages from Snowdonia. Further work may reveal more. Such diversity obviously indicates that the original crinoid fauna was varied, even after accounting for taphonomic losses, as one crinoid species could not contribute over fifty differing columnal morphotypes. This diversity, however, must be interpreted with care. Certain species possess xenomorphic stems (Moore and Jeffords 1968; Moore *et al.* 1968; Ubaghs 1978a) in which columnals undergo shape changes along the stem (Manten 1970; Rasmussen 1978a). Proxistele, mesistele, and dististele often contain distinctive columnal morphotypes, e.g. *Scyphocrinites* (Ubaghs 1978b, T490), *Bathyrinus* (Macurda and Meyer 1976; Rasmussen 1978b, T843–T846), and *Archaeataxocrinus* (Lewis 1981). The ornament of the articular facets may differ in the proxistele, mesistele, and dististele. Columnals from the zone

of maximum flexibility in the stem (middle 67–75% of the stem in camerates—Seilacher *et al.* 1968; Brower 1978) may possess specialised features on these facets.

Different types of ornamentation of the articular facets are observed during growth in isocrinid articulates (Rasmussen 1978*b*, T270) and *Bathyrinus* (Macurda and Meyer 1976). *Kallimorphocrinus* has smooth and nodose articular facets that are often found on opposing sides of the same columnal (Lane and Sevastopulo 1981). Crinoids with heteromorphic stems, i.e. stems composed of dissimilar columnals classifiable as nodals and one or more orders of internodals (Webster 1974), could potentially yield several distinctive columnal morphotypes. Preservation controls the precision of morphotype identifications. Poor preservation destroys delicate ornamentation and thus some morphotypes may be poorly preserved varieties of others.

After considering these factors, it is believed that the diversity of the columnals can be attributed to the presence of several crinoid species within the Caradocian sessile benthos and also to morphological differences between the columnals of these species.

FURTHER APPLICATIONS

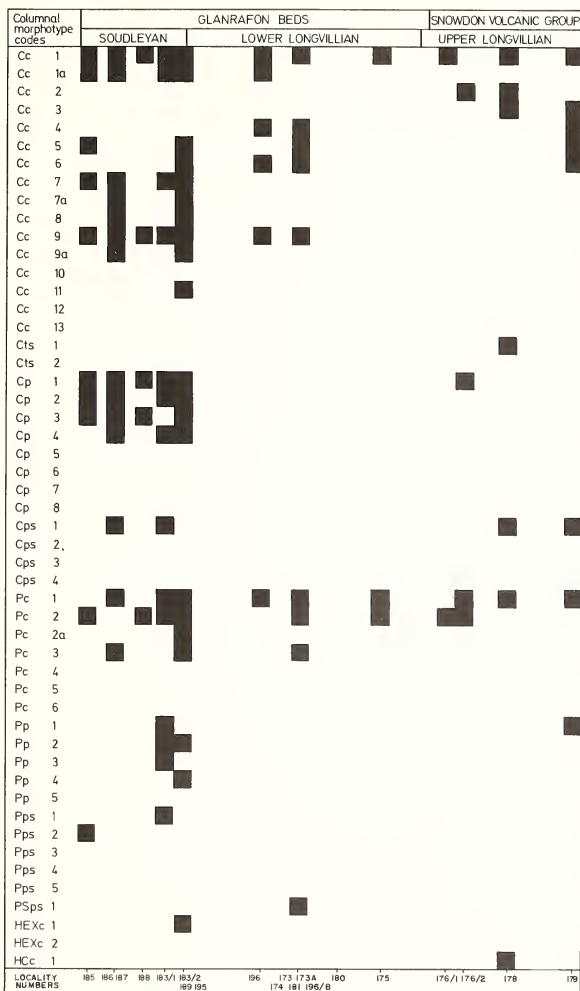
The list of columnal morphotypes provides a method of quantifying the occurrence of crinoid columnals and a relative appreciation of their diversity. Other applications also present themselves. Through computerized techniques, temporally and spatially recurrent morphotype combinations may be recognized. Such combinations may represent the columnals originally comprising either the heteromorphic or xenomorphic stems of certain crinoid species. Once these combinations are statistically proven to be recurrent, it may be that these combinations could be assigned generic names. Certain morphotypes in the list are differentiated only on minor morphological details, e.g. Cc 7 and Cc 7a, Cc 9 and Cc 9a, Cp 4 and Cp 5, and Pc 2, Pc 2a, and Pc 6. Such combinations possibly represent original columnal transitions along stems. If, as Stukalina (1966) believes, the transverse outline of the lumen is a relatively stable morphological feature, it is feasible that, for example, the Cps or Pps genus groups were components of either a heteromorphic or xenomorphic stem. The abundance and diversity of the Snowdonian columnals favours them as biostratigraphical indicators and subsequently they may corroborate existing Snowdonian biostratigraphies (Wright 1979) although, like the shelly macrofauna, the crinoids were probably facies controlled. Morphotypes from contemporaneous rocks within the Anglo-Welsh province are easily accommodated within the list (S. Donovan, pers. comm.) and morphotype correlations may be possible between Snowdonia and these areas.

To demonstrate these applications, the presence and absence of columnal morphotypes, from assemblages collected from the Glanrafon Beds and Snowdon Volcanic Group to the south-west of Dolwyddelan, are plotted. The resultant plot (text-fig. 5) shows several features:

- (a) Certain morphotypes appear potentially useful biostratigraphical indicators, as they seem restricted either to one horizon or Stage, e.g. Cc 2, Cc 3, Cc 7, Cc 7a, Cc 8, Cc 9a, Cc 11, Cts 1, and Cp 1-4.
- (b) Certain morphotypes appear to cluster together, e.g. Cc 4-6, Cp 1-4, and Pc 1-2, and may represent original morphotype combinations from xenomorphic or heteromorphic stems.
- (c) The Soudleyan-lower Longvillian stage boundary was derived from the shelly macrofauna, prior to the plotting of the presence-absence data. These data reveal a significant change in the stratigraphical distribution of morphotypes at this horizon.

SUMMARY

In contrast to many similar analyses, dissociated crinoid columnals and other fragmented fossils are incorporated within faunal analyses of the Caradoc shelly assemblages from Snowdonia. A list is compiled for the different columnal morphotypes encountered within the Snowdonian shelly faunas, which aids identification and highlights columnal diversity (fifty-one morphotypes). Taking into account xenomorphism, heteromorphism, taphonomic losses, and the vagaries of preservation, it is considered that several crinoid species comprised part of the sessile benthos in the outer



TEXT-FIG. 5. Presence-absence plot of columnal morphotypes from the Glanrafon Beds and Snowdon Volcanic Group to the south-west of Dolwyddelan.

sublittoral–offshore environments of the north-western part of the Welsh Basin. Further applications of the list include the potential recognition of columnal combinations which originally may have comprised either heteromorphic or xenomorphic stems and the possible use of columnals in biostratigraphy and resultant correlations.

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THE ORDOVICIAN-SILURIAN BOUNDARY GRAPTOLITE FAUNA OF DOB'S LINN, SOUTHERN SCOTLAND

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ABSTRACT. The strata at Dob's Linn from the Extraordinarius Band of the Upper Hartfell Shale Formation to 2.3 m above the base of the Birkhill Shale Formation and their contained taxa are described and accurate faunal ranges provided. The boundary separating the *Climacograptus? extraordinarius* and *Glyptograptus persculptus* zones occurs within a 1.17 m thick unfossiliferous part of the succession. The boundary between the *G. persculptus* and *Parakidograptus acuminatus* zones is defined at 1.6 m above the base of the Birkhill Shale in the Linn Branch section, where *Akidograptus ascensus* and *P. acuminatus* s.l. first occur. A member of the *Glyptograptus?* 'venustus' group is recorded from Britain for the first time. Accurate correlation is attempted with zonal sequences in Soviet central Asia, central China, and eastern Canada.

STUDIES by Toghil (1968*a, b*, 1970) and more recently by Ingham (1979) have shown that much research remains to be done at the classic locality of Dob's Linn near Moffat, southern Scotland, although the pioneering work by Lapworth (1878) and taxonomic descriptions by Elles and Wood (1901-18) still form a good foundation. Present debate surrounding the Ordovician-Silurian boundary renders the need for detailed study of all possible stratotype sections. Thus the succession at Dob's Linn from the top of the Upper Hartfell Shale Formation up to unequivocal *P. acuminatus* Zone strata in the Birkhill Shale Formation was examined in order to cover all possible horizons being considered for a future-defined Ordovician-Silurian boundary.

The least tectonically affected section through these strata at Dob's Linn is on the north bank of the Linn Branch, where a continuous section has now been excavated (Williams 1980, loc. 5); all measurements and most of the material referred to here originate from this 'Linn Branch trench'. During collecting bulk samples were made, either of a single black shale band in the Upper Hartfell Shale, or of a convenient interval, normally about 15 cm thick, in the continuously black Birkhill Shale. These were split in the laboratory and all slabs examined with a binocular microscope. This method ensured maximum recovery of specimens and obviated damage during transport from the field. Although such a technique commonly limited the accuracy with which horizons could be located to the thickness of the sampling interval, this disadvantage was easily outweighed by the more efficient recovery of rare specimens. Critical intervals could also be recollected in greater detail.

STRATIGRAPHY

Upper Hartfell Shale Formation

The Upper Hartfell Shale consists of some 28 m of mostly pale grey, barren mudstone or shale. There are, however, three intervals containing black shale bands, named the Complanatus, Anceps, and Extraordinarius bands after their respective zonally diagnostic faunas. The two Complanatus Bands occur just over 9 m above the base of the Upper Hartfell Shale (as defined in Williams 1982*a*) and yield the typical *Dicellograptus complanatus* Zone fauna. They are followed by approximately 13 m of apparently unfossiliferous pale grey mudstone before the first of the Anceps Bands. The five bands A to E have now been subdivided into two subzones of the high *D. anceps* Zone (Williams 1982*b*); bands A and B are contained within the *D. complexus* Subzone, whilst bands C to E are accommodated within the *Paraorthograptus pacificus* Subzone (text-fig. 2). The top Anceps Band (E) yields the lowest known specimens of *C? extraordinarius* (Sobolevskaya, 1974). It is followed by

0.96 m of unfossiliferous pale grey mudstone before the thin dark-brown Extraordinarius Band, first discovered by Ingham (1974). This contains rare diplograptids, especially in the Long Burn section (Williams 1980, loc. 7), which Rickards (1979) identified as *C? extraordinarius* (Sobolevskaya, 1974), *Climacograptus* cf. *normalis* Lapworth, 1877, and *Glyptograptus* cf. *persculptus* (Salter, 1865). It is here concluded that tectonic deformation of this band is too great to allow even generic determination of many specimens, although the characteristic fusiform outline of *C? extraordinarius* permits identification of this species. The faunal assemblage indicates the late Ordovician *C? extraordinarius* Zone, described from the north-eastern U.S.S.R. by Koren' *et al.* (1979) and others. Owing to the first occurrence of *C? extraordinarius* in Anceps Band E, it is likely that the *D. anceps*-*C? extraordinarius* zonal boundary lies within the pale, unfossiliferous mudstone a short distance above Anceps Band E. Intensive study between this band and the base of the Birkhill Shale has failed to reveal any additional graptolite bands.

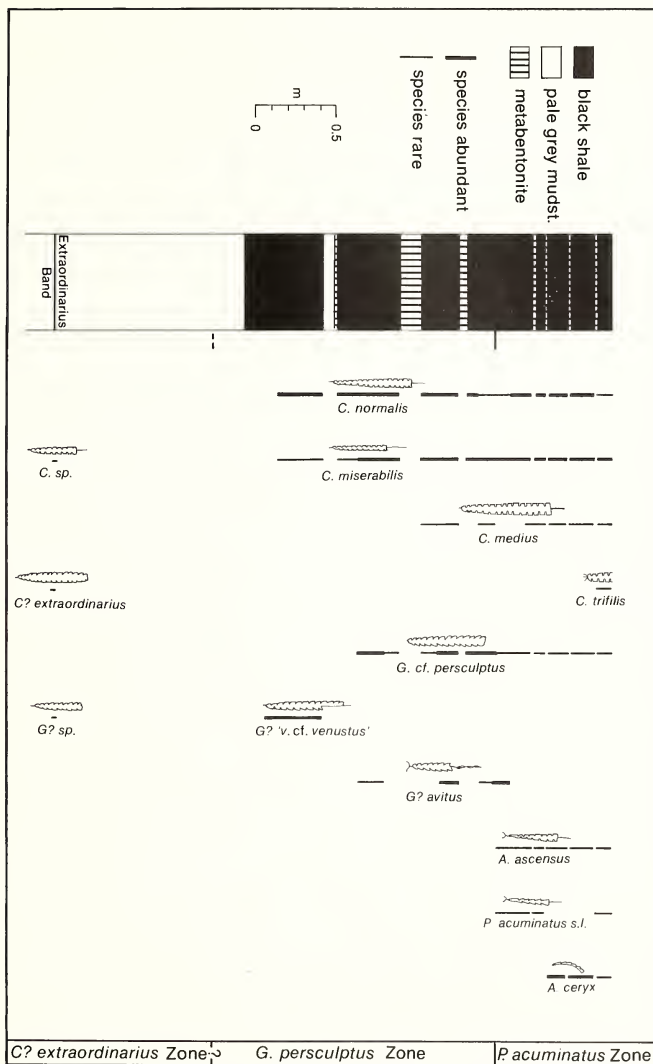
Birkhill Shale Formation

The 43 m of Birkhill Shale (Toghill 1968b) are composed predominantly of black graptolitic shale or mudstone. They also contain thin metabentonite seams, which have commonly acted as planes of bedding slip, and occasional pale grey-green mudstones which become common in the *Monograptus convolutus* and *M. sedgwickii* zones and dominant in the *Rastrites maximus* Zone. The mudstones then give way transitionally into the Gala Greywacke Group, which at Dob's Linn begins within the *R. maximus* Zone.

The junction between the pale grey mudstones of the Upper Hartfell Shale and the black shales and mudstones of the Birkhill Shale is sharp and occurs 1.17 m above the Extraordinarius Band in the Linn Branch section (text-fig. 1). The basal 15 cm of black shale are unfossiliferous and coarse with a fine mottled appearance. They are followed by more typical graptolitic black shale, although this again is mottled and contains common bands of silty material. This basal interval is probably the one referred to by Elles and Wood (1906, p. 186) as the 'gingerbread' bed at the base of the Birkhill Shale, which they recorded as containing abundant *C. normalis* Lapworth, 1877. At 0.2 m above the base typical black graptolitic shale is present, yielding a fairly abundant fauna of *C. normalis* and *G? 'venustus* cf. *venustus*' (Legrand, 1976), with rarer specimens of *C. miserabilis* Elles and Wood, 1906. At 0.46 m there is a sharp reversion to pale grey-green mudstone, followed by 10 cm of variously coloured and laminated mudstones. At 0.56 m these are overlain by a thin metabentonite, which is followed by typical black graptolitic shale. *G? 'v. cf. venustus*' last occurs just below the pale mudstone unit, whilst *C. normalis* and *C. miserabilis* continue into the overlying black shale. At about 0.6 m is a silty horizon containing beautifully preserved, three-dimensional specimens of *C. normalis*. *C. miserabilis* becomes abundant by about 0.7 m and remains so throughout the remainder of the collected interval, while *Glyptograptus* cf. *persculptus* (Salter, 1865) and *G? avitus* Davies, 1929 first appear at this horizon.

A thick metabentonite occurs from 0.96 to 1.1 m; it contains irregular slivers of black shale and has evidently acted as a plane of bedding slip. However, it appears to be concordant with the bedding and it is unlikely that it has had any significant effect on the succession. Possible specimens of *C. medius* Törnquist, 1897 first appear just above the metabentonite, but they are rather narrow and may represent tectonically widened specimens of *C. normalis*. Definite specimens of *C. medius* appear soon after and occur sporadically throughout the remainder of the collected interval. *G? avitus* first becomes abundant at 1.2 m.

Another metabentonite is present from 1.32 to 1.38 m but no significant faunal changes occur until 1.6 m when *Akidograptus ascensus* Davies, 1929 and *Parakidograptus acuminatus* (Nicholson, 1867) *s.l.* first appear and where *G? avitus* was last seen in the present study. Davies, however, recorded his holotype as coming from the '*A. acuminatus* Zone' (see systematic description) while Stein (1965) and Rickards (1976a) also recorded *G? avitus* from the *P. acuminatus* Zone elsewhere. The appearance of *A. ascensus* is considered by most workers on lower Silurian graptolites to mark the base of the *P. acuminatus* Zone; whilst this effectively means that the *G. persculptus*-*P. acuminatus* zonal boundary is defined on the appearance of a single species, it appears to be a synchronous,



TEXT-FIG. 1. Lithological succession and species ranges of the top Lower Hartfell Shale and basal Birkhill Shale in the Linn Branch trench.

cosmopolitan event when compared with other recorded graptolite ranges. It is here suggested that the base of the *P. acuminatus* Zone should be defined at 1.6 m above the base of the Birkhill Shale in the Linn Branch section at Dob's Linn. Toghill (1968a, b) previously defined the base of the *P. acuminatus* Zone, employing the same criteria, at only 1.06 m above the base of the Birkhill Shale, using sections on the Main Cliff and on the 'North Cliff' (some 20 m north along strike from the Linn Branch section). The most recent description given by Toghill on the basal Birkhill Shale succession was in Cocks *et al.* (1970, p. 83); here it was stated that 'the basal bed is a conspicuous 10 cm (4 in) hard grey silty mudstone which yields abundant specimens of *Climacograptus scalaris normalis* in half-relief . . . and has recently yielded *Glyptograptus persculptus* itself'. No mention was made of the basal mottled, unfossiliferous unit, the lowest strata with poorly preserved *C. normalis* and *C. miserabilis*, or the temporary reversion to an Upper Hartfell-type of lithology. As stated above, the silty horizon containing three-dimensional specimens of *C. normalis* was found during the present study at about 0.6 m, just above a metabentonite which directly follows the lithological reversion to pale grey mudstone (text-fig. 1). I conclude that the 'basal bed' of the Birkhill Shale recorded by Toghill (1968a, b) and Cocks *et al.* (1970) was in fact the black shale overlying the lithological reversion and that the lowest part of the Birkhill Shale underlying this unit was either missed during collecting or was faulted out of their sections. If these strata (0.58 m) are added to Toghill's 1.06 m a true thickness of 1.64 m is obtained, corresponding closely to that found during the present study. Confirmation of this hypothesis is apparently found in Toghill (1968b, text-fig. 2) which shows only two metabentonites ('claystones' of Toghill) in the *G. persculptus* Zone in positions corresponding to those found by the present author above the lithological reversion.

A. ascensus seems to occur consistently earlier and more commonly than *P. a. acuminatus* in the low *P. acuminatus* Zone (Davies 1929, p. 10; Toghill 1968b, p. 658; Hutt 1974, p. 6; Oradovskaya *et al.* 1979, field guide range chart). It is probable that the *P. acuminatus* Zone could be formally divided into two subzones after detailed collecting of the remainder of this zone at Dob's Linn.

The early monograptid *Atavograptus ceryx* (Rickards and Hutt, 1970) is crowded on a few bedding planes from about 1.9 to 2.1 m, whilst occasional specimens occur above this level. Several fragments of an indeterminate *Atavograptus* have also been found (text-figs. 9i, j). Monograptids have not been recorded previously lower than the *Cystograptus vesiculosus* Zone at Dob's Linn (Toghill 1968a, p. 48), although Rickards and Hutt (1970) and Hutt (1974) recorded *A. ceryx* from both the *G. persculptus* and *P. acuminatus* zones of the English Lake District. Only one specimen of *Climacograptus trifilis* Manck, 1923 was found, in the interval 2.19 to 2.31 m; this species is considered to be restricted to the *P. acuminatus* Zone (Stein 1965, p. 168; Toghill 1968b, p. 658). Toghill (1968b) also recorded *Diplograptus m. modestus* Lapworth, 1876 and *D. modestus parvulus* H. Lapworth, 1900 to occur throughout the *G. persculptus* and *P. acuminatus* zones at Dob's Linn, as did Jones (1909) from equivalent strata in mid Wales. No specimens resembling this large diplograptid or its subspecies have, however, been found, neither have forms corresponding to *C. indivisus* Davies, 1929, recorded to occur in the *G. persculptus* Zone of Dob's Linn by Rickards (1976a, p. 157). The enigmatic fossil *Dawsonia campanulata* Nicholson, 1873 occurs fairly commonly from 1.9 to 2.1 m, but the affinity and stratigraphical range of this form are still unknown.

Discussion of correlation chart (text-fig. 2)

The original top Ordovician and basal Silurian British graptolite zones identified by Lapworth (1878) and Elles and Wood (1901-18) have since been somewhat modified. Jones (1909) recognized the *G. persculptus* Zone as a clearly distinguishable part of the *P. acuminatus* Zone *sensu* Elles and Wood in the Welsh succession and this division has since been recognized in Ordovician-Silurian successions around the world. Rickards (1979) established the presence of the *C? extraordinarius* Zone at Dob's Linn, represented by the impoverished fauna of the Extraordinarius Band. Williams (1982b) subdivided the Anceps Bands at Dob's Linn into the *Dicellograptus complexus* (Bands A and B) and *Paraorthograptus pacificus* (Bands C to E) subzones.

The discrepancies resulting from equating lithostratigraphical units, shelly fossil stages, and graptolite zones have caused confusion concerning the position of the Ordovician-Silurian

		DOB'S LINN succession	SCOTLAND	N. AMERICA Riva 1974, 1981	U.S.S.R. Koren' et al. 1979	CHINA Mu et al. 1980
LLANDOVERY	RHUDDANIAN	Birkhill Shale	P. acuminatus	?	A? acuminatus	A? acuminatus
			G. persculptus	G. persculptus	G? persculptus	G. persculptus
ASHGILL	HIRNANTIAN	Extraordinarius		- ? -	-----	-----
		Band	C? extraordinarius	A. inuiti	C? extraordinarius	D. bohemicus
	RAWTHEYAN	Upper Hartfell Shale		- ? -	-----	-----
		E	P. pacificus	D. complanatus	P. pacificus	P. uniformis D. mirus T. typicus
		D				
		Anceps Bands	C			
		B	D. anceps	C. longispinus	C. longispinus	D. szechuanensis
		A				
		not to scale	D. complexus			

TEXT-FIG. 2. Correlation of the Dob's Linn succession with shelly stages and graptolite zonal sequences elsewhere. Dotted boundaries for Scottish zones indicate that zonal boundaries lie within unfossiliferous parts of the succession and may not be determined accurately. Dashed lines in other columns indicate uncertain correlation with the Scottish zonal sequence (correlation with North America is tentative).

boundary. Correlation of the shelly fossil stages with the graptolite zonation is discussed by Williams (in press; 1982b). In Kazakhstan (Koren' et al. 1979) and eastern North America (Léspérance and Sheehan 1981) the *C? extraordinarius* Zone and equivalent strata lie entirely within the Hirnantian Stage, which has also been recorded to encompass portions of the *P. pacificus* Subzone and *G. persculptus* Zone. Rickards (1982) states, however, that specimens from Kazakhstan which were previously named as *G. persculptus* do not belong to this taxon and may be referable to *C? extraordinarius*. This implies that the whole of the *G. persculptus* Zone may fall within the Llandovery, although Léspérance and Sheehan (1981, p. 231) record '*C. v. venustus*' in association with a *Mucronaspis* [*Dalmanitina*] trilobite fauna referable to the Hirnantian Stage. Clearly additional work needs to be published before any reliable correlation between the shelly and graptolitic biostratigraphy at this level can be demonstrated. The Hirnantian-Rhuddanian boundary is unlikely to coincide with either the *C? extraordinarius*-*G. persculptus* zonal boundary or the Upper Hartfell Shale-Birkhill Shale lithological boundary. The junctions between the *P. pacificus* Subzone, *C? extraordinarius* Zone, and *G. persculptus* Zone are at unknown horizons in the pale grey, non-graptolitic lithology of the Upper Hartfell Shale and cannot be defined accurately in southern Scotland.

Riva (1981) added the zone of *G. persculptus* to the zonal scheme that he erected for eastern North America in 1974, owing to the presence of '*C. v. venustus*' in the Gaspé Peninsula. Riva and Petryk (1981) renamed the *C. prominens*-*C. elongatus* Zone the *Amplexograptus inuiti* Zone, as the last species proved to be a senior synonym of the other two. The *A. inuiti* Zone of Anticosti Island and

other north-eastern American localities yields *Orthograptus? abbreviatus* Elles and Wood, 1907, a species known from much of the *D. anceps* Zone in Britain; specimens recorded from the *P. acuminatus* Zone by Toghiani (1968b) and Hutt (1974) are now considered to belong to a separate diplograptid lineage. The *A. inuiti* Zone also contains the apparently endemic taxa *Peiragraptus fallax* Strachan, 1954, *G. ex gr. lorrainensis* (Ruedemann, 1925), and *A. inuiti prominens* (Barras, 1954) in addition to *A. i. inuiti* (Cox, 1933) itself. Koren' *et al.* (1980, p. 125 footnote) acknowledged Koren's joint work with Riva, which established that *A. i. inuiti* was a senior synonym of *A. stukalinae* Mikhaylova, 1973 from the *C. longispinus supernus* Zone of Kazakhstan.

Riva (1974) stated that the '*C. prominens-elongatus* Zone' (= *A. inuiti* Zone) might correlate with the 'barren interval between the *D. anceps* and *G. persculptus* Zone of the Moffat Region'. Although *O? abbreviatus* and *A. i. inuiti* suggest a horizon equivalent to part of the *D. anceps*-*C. longispinus supernus* Zone, the lack of any other late Ordovician taxa characteristic of these intervals suggests a correlation with the *C? extraordinarius* Zone. Except for its base, the underlying *D. complanatus* Zone (*sensu* Riva) contains only rare graptolites and the position of the boundary with the *A. inuiti* Zone appears uncertain. In the Gaspé Peninsula the boundary between the *A. inuiti* and *G. persculptus* zones is apparently defined on the first appearance of *G? 'v. venustus'* and *C. normalis s.s.* (Riva 1981), although the only evidence given by Riva and Petryk (1981) for the 'Silurian' on Anticosti Island is the presence of *C. normalis s.s.* (known to occur in the Ordovician Anceps Bands at Dob's Linn) and the absence of the *A. inuiti* zonal fauna. Although the presence of *G? 'v. venustus'* is likely to prove useful in the future, the first occurrence has not yet been determined in a continuously graptolitic sequence elsewhere, and is therefore of little help at present. It is evident that the Ordovician-Silurian boundary graptolite succession at Anticosti Island is poor, and that correlation with graptolite zonal sequences elsewhere is rather tentative.

Koren' *et al.* (1979) gave a summary of the upper Ordovician to basal Silurian graptolite biostratigraphy in the central Asian part of the U.S.S.R. with detailed range charts of the *C. longispinus supernus* to '*Akidograptus? acuminatus* zones. The *C. longispinus supernus* Zone is divided into a lower *C. longispinus* and an upper '*Pacificograptus? pacificus* Subzone. The *C. longispinus* Subzone contains *D. complanatus* Lapworth, 1880, *D. aff. complanatus*, *C. longispinus longispinus* Hall, 1902, *C. longispinus supernus* Elles and Wood, 1906, *C. ex gr. longispinus*, *C. hastatus* Hall, 1902, and *Orthograptus? ex gr. amplexicaulis* (Hall, 1847). By comparison with the Australian succession (Vandenberg 1981), this fauna indicates an interval approximating to the *D. complanatus* and lower *D. anceps* zones of Britain, although the exact correlation is uncertain. It is succeeded by the *P. pacificus* Subzone which contains a diverse fauna including *D. ornatus* Elles and Wood, 1904, *C. longispinus supernus*, *C. hastatus*, *C. normalis*, *P. pacificus* subsp., and *Plegmatograptus? lautus* Koren' and Tzai, 1980, indicating an interval equivalent to the *P. pacificus* Subzone of Dob's Linn.

The *C. longispinus supernus* Zone is followed by that of *C? extraordinarius* which yields only the zonal species, *C. normalis* Lapworth, 1877, *C. angustus* (Perner, 1895) [= *C. miserabilis* Elles and Wood, 1906], and *Glyptograptus* sp. in the lower part, and only *C. normalis* and *C. angustus* with rare *Glyptograptus* spp. in the upper part. This zone correlates with the *C? extraordinarius* Zone of Dob's Linn, where the Extraordinarius Band probably lies in the lower part of the zone. The transition into the following '*G? persculptus* Zone appears diffuse, and seems to rely solely on the common occurrence of *G. persculptus s.l.* The succeeding '*A? acuminatus* Zone is defined by the first appearance of *Akidograptus* and a variety of diplograptids not yet recognized in Britain.

Several papers giving the zonal scheme for the top Ordovician and basal Silurian of central China have been published, including a summary in English by Mu *et al.* (1980). The most detailed report in English is, however, given by Mu (1980), although this only gives faunal lists for the *Diplograptus bohemicus* and *G. persculptus* zones. Wang and Zhao (1978) and other regional handbooks record the *Dicellograptus szechuanensis* Zone to contain *D. szechuanensis* Mu, 1954 [= *D. complexus* Davies, 1929], *C. longispinus*, and *O? abbreviatus* and the top is almost certainly equivalent to the top of the *D. complexus* Subzone at Dob's Linn. The following three zones of *Tangyagraptus typicus*, *Diceratograptus mirus*, and *Paraorthograptus uniformis* seem to differ only by the occurrence of each zonal species, although the first two apparently belong to rather strange, endemic Chinese dicranograptid

genera. The three zones are considered here to merit only subzonal status. All three contain *Paraorthograptus* spp. and probably equate with most of the *P. pacificus* Subzone of Dob's Linn. Li and Ge (1981) record a new species, *Akidograptus antiquus*, from the *T. typicus* 'Zone'. All previous records of *Akidograptus* have been restricted to the Silurian; if this species is a true member of the genus the stratigraphical significance of *A. ascensus* becomes solely at the specific level.

Mu (1980) records the *D. bohemicus* Zone to contain *Dicellograptus* spp., *C. longispinus supernus*, *Glyptograptus* spp., *Diplograptus bohemicus* (Marek, 1955), *D. orientalis* Mu *et al.*, 1974 [? = *C? extraordinarius*], *Paraorthograptus* sp., and '*Paraplegmatograptus*' sp. Mu (pers. comm.) considers *D. orientalis* to be close to, or even conspecific with, *C? extraordinarius*. If this is correct the faunal assemblage is very similar to that of Anceps Band E at Dob's Linn and it seems likely that the *D. bohemicus* Zone of China correlates with the top *P. pacificus* Subzone and much of the *C? extraordinarius* Zone of Scotland. The following *G. persculptus* Zone contains *C. cf. normalis*, *C. miserabilis*, *G. persculptus*, and *A. ascensus*. The firm assertion of Mu (1980) to include the first occurrence of *A. ascensus* within his *G. persculptus* Zone differs from the ideas of Koren' and most fellow Soviet workers and the present author, and means that the base of the '*A?*' *acuminatus* Zone is higher in China than elsewhere. Mu combines the first occurrence of *A. ascensus* with the fact that monograptids first appear in the *G. persculptus* Zone (Rickards and Hutt 1970) to argue that the *G. persculptus* Zone should be assigned to the basal Silurian. He also considers that the break between the Chinese '*Hirnantia*' and Silurian '*Protatrypa*' shelly assemblages occurs at the same horizon as the boundary between the *D. bohemicus* and *G. persculptus* zones.

SYSTEMATIC PALAEOLOGY

Specific diagnoses are revised unless otherwise stated. Terminology follows that of Bulman (1970). Most material is from the author's collection, housed in the Hunterian Museum, Glasgow University (HM). Other specimens are from Birmingham University (BU), Sedgwick Museum, Cambridge (SM), British Museum (Natural History) (BM), and Institute of Geological Science, South Kensington (GSM). Stratigraphical intervals recorded refer to the height above the base of the Birkhill Shale.

Family DIPLOGRAPTIDAE Lapworth, 1873

Genus CLIMACOGRAPTUS Hall, 1865

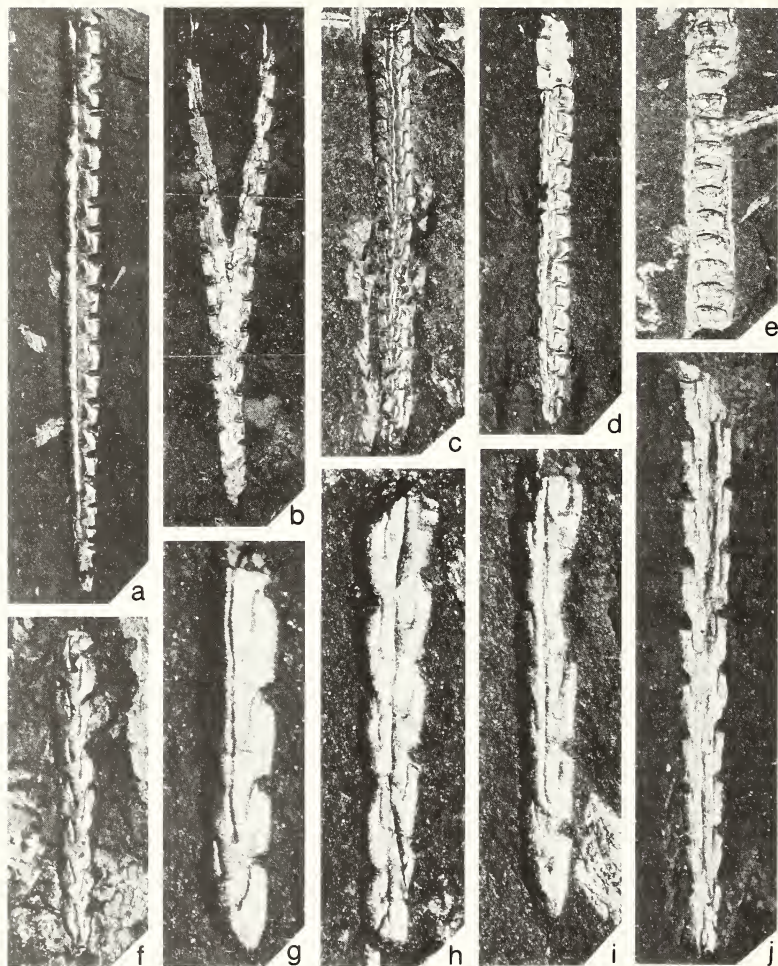
Type species (by original designation). *Graptolithus bicornis* Hall 1847, p. 268, pl. 73, fig. 2 (*pars*-Riva 1974).

Diagnosis (from Bulman 1970, p. V125). Rhabdosome nearly circular in cross-section, scalariform views consequently common; thecae strongly geniculate, with deep apertural excavations, supra-geniculate walls straight, parallel to axis of rhabdosome.

Climacograptus normalis Lapworth, 1877

Text-figs. 3a-e, 4a-e, 7g

- 1877 *Climacograptus scalaris* var. *normalis* Lapworth, p. 138, pl. 6, fig. 31.
- ?1897 *Climacograptus scalaris* var. *normalis* Lapworth; Perner, p. 7, pl. 10, fig. 1.
- 1906 *Climacograptus scalaris* (Hisinger) var. *normalis* Lapworth; Elles and Wood, p. 186, pl. 26, fig. 2a-g; text-fig. 119a-d.
- 1922 *Climacograptus scalaris* His. sp. var. *normalis* Lapworth; Gortani, p. 104, pl. 17, fig. 23.
- 1924 *Climacograptus scalaris normalis* Elles and Wood; Hundt, p. 55, pl. 1, figs. 28-31.
- 1929 *Climacograptus scalaris* var. *normalis* Lapworth; Davies, p. 8, text-fig. 29.
- 1929 *Climacograptus scalaris*-*C. medius* transient; Davies, text-figs. 28, 31.
- 1934 *Climacograptus scalaris* var. *normalis* Lapworth; Hsü, p. 60, pl. 4, fig. 8a-i.
- 1945 *Climacograptus scalaris* var. *normalis* Lapworth; Waterlot, pl. 4, fig. 92.
- 1948 *Climacograptus* (*Climacograptus*) *scalaris normalis* Lapworth; Přibyl, p. 17.
- 1948 *Climacograptus scalaris* v. *normalis*; Waern, p. 449, pl. 26, fig. 1; text-fig. 5.
- 1952 *Climacograptus scalaris normalis* Lapworth; Münch, p. 50, pl. 1, fig. 5a, b, ?c.
- 1963 *Climacograptus scalaris* cf. var. *normalis*? Lapworth; Willefert, p. 14, text-fig. 5.



- 1965 *Climacograptus scalaris normalis* Lapworth; Stein, p. 157, pl. 14c, text-figs. 13, 14a-e, tables 3, 4.
 1970 *Climacograptus normalis* Lapworth; Rickards, p. 28, pl. 1, figs. 1, 7, 8; text-fig. 13, figs. 7, 8.
 1974 *Climacograptus normalis* Lapworth; Hutt, p. 19, pl. 1, figs. 8, 9; pl. 2, figs. 1-4.
 ?1978 *Climacograptus* cf. *normalis* Lapworth; Wang and Zhao, p. 638, pl. 206, fig. 12.

Holotype. BU 1136, the specimen possibly figured by Lapworth (1877, pl. 6, fig. 31). The original illustration is insufficient to determine whether this or the other specimen on the slabs (part and counterpart) is his figured specimen, but I consider this to be the most likely one. Also figured by Elles and Wood (1906, pl. 26, fig. 2a) and this paper (text-fig. 4a). From the Birkhill Shale, Dob's Linn.

Material. Several specimens from the C. Lapworth and H. Lapworth collections (BU) and numerous specimens preserved both flattened and in relief from my own collections.

Horizons and localities. The basal 2-3 m of Birkhill Shale, *G. persculptus* and low *P. acuminatus* zones, Dob's Linn.

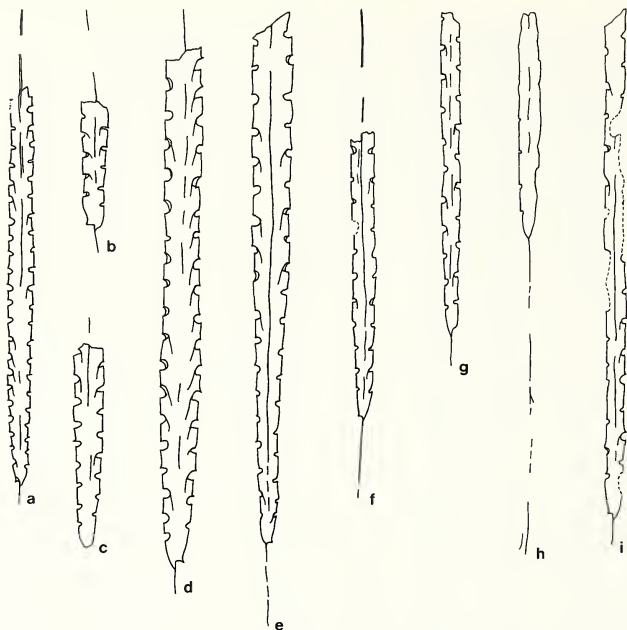
Diagnosis. Rhabdosome over 30 mm long with a normal maximum undeformed width of 1.5 mm attained within 15 mm. Thecae of *Climacograptus* style, numbering nine to eleven in 10 mm (undeformed). Virgella and nema long.

Description. The rhabdosome is over 30 mm long. It measures about 0.7 mm at the aperture of th^1 in tectonically undeformed specimens (range 0.6-1.1 mm), widening to 1.1-1.6 mm in 5 mm and reaching the maximum width (characteristically 1.5 mm when undeformed) within 10 mm. Proximally the thecae number ten to thirteen in 10 mm, reducing distally to eight to twelve in 10 mm (commonly nine in 10 mm when undeformed). The holotype is tectonically widened with a maximum width of 2 mm. The sicula is exposed in obverse view for 1.0-1.3 mm, which may represent its entire length. It possesses a long virgella which sometimes exceeds 10 mm long. th^1 and th^2 grow upwards for most of their length; the wall of the sicula on the side of th^2 is normally free for 0.15-0.2 mm, resulting in a slight 'notch' at the base of the supragenicular wall of th^2 . The thecae are sub-alternate and typically *Climacograptus* in style with angular sigmoidal curvature. The supragenicular walls are normally straight, vertical, and with thickened genicular hoods producing sharp genicula. The apertures are horizontal or very slightly everted and open into excavations which occupy one-quarter of the total rhabdosome width proximally and one-fifth distally, although they appear deeper when the rhabdosome is preserved obliquely. A distally free nema is invariably present and may reach several centimetres long.

Remarks. The specimens of *C. normalis* described here show clearly the difference between the internal and external moulds of graptolites when preserved in relief. The internal moulds (e.g. text-fig. 3c, d) show prominent intertheatal septa, while the external moulds (e.g. text-figs. 3a, 7g) have smoothly rounded stipes and the junctions of the intertheatal septa with the outer walls are only indicated by shallow, rounded depressions.

C. normalis may be confused with *C. miserabilis*, *C. medius* Törnquist, 1897, *C. rectangularis* (M'Coy, 1850), *Glyptograptus?* *avitus*, and *G?* 'v. cf. *venustus*' when the specimens have suffered tectonic distortion. It may normally be separated from *C. miserabilis* by its more gradual widening and maximum width, which normally exceeds 1.2 mm even when tectonically stretched, in comparison with the usual 1 mm maximum width of *C. miserabilis*. *C. medius* has a more robust form

TEXT-FIG. 3. All except *b* from the Linn Branch trench, Dob's Linn. *a-e*, *Climacograptus normalis* Lapworth, 1877, $\times 5$. *a*, HM C13955a, external mould in relief, slightly oblique orientation, 1.88-2.0 m, *P. acuminatus* Zone. *b*, BU 1142b, mutation showing distal forking; note formation of two nemata, Birkhill Shale, Dob's Linn, H. Lapworth Collection; counterpart figured (proximal only) Elles and Wood (1906, text-fig. 119b). *c*, HM C13759/1a, internal mould in partial relief, silty horizon at 0.6 m, *G. persculptus* Zone. *d*, HM C13756, internal mould in partial relief, oblique orientation, silty horizon at 0.6 m, *G. persculptus* Zone. *e*, HM C13787a, flattened distal fragment in scalariform orientation, 0.7-0.85 m, *G. persculptus* Zone. *f-i*, *Climacograptus miserabilis* Elles and Wood, 1906. *f*, HM C13788, reverse view, in partial relief, 0.7-0.85 m, *G. persculptus* Zone, $\times 10$. *g*, HM C13971, reverse view, in full relief; note terminal thickened node of median septum, 1.88-2.0 m, *P. acuminatus* Zone, $\times 20$. *h*, HM C13964, obverse view, in full relief, 1.88-2.0 m, *P. acuminatus* Zone, $\times 20$. *i*, HM C14004, reverse view, in full relief, 2.01-2.14 m, *P. acuminatus* Zone, $\times 20$. *j*, *Climacograptus miserabilis* Elles and Wood?, HM C13752, obverse view, in partial relief, 0.35-0.56 m, *G. persculptus* Zone, $\times 10$.



TEXT-FIG. 4. All $\times 5$ except fig. *a*. *a*-*e*, *Climacograptus normalis* Lapworth, 1877. Dob's Linn (*b*-*e* from the Linn Branch trench). *a*, BU 1136, Holotype?, note basal notch on wall of th¹₂; Lapworth's original illustration is insufficient to determine whether this or the other specimen on the slab is his figured specimen; figured Lapworth (1877, pl. 6, fig. 31)?, counterpart figured Elles and Wood (1906, pl. 26, fig. 2*a*), $\times 2.5$. *b*, HM C13872*b*, juvenile rhabdosome, 1.38-1.46 m, *G. persculptus* Zone. *c*, HM C13613, Anceps Band D, Upper Hartfell Shale, *P. pacificus* Subzone. *d*, HM C13732*a*, specimen with rapid widening, 0.2-0.35 m, *G. persculptus* Zone. *e*, HM C13838, specimen with only gradual widening, 1.2-1.32 m, *G. persculptus* Zone. *f*-*i*, *Climacograptus miserabilis* Elles and Wood, 1906, Linn Branch trench, Dob's Linn. *f*, HM C13938, specimen with long virgella and nema, 1.69-1.79 m, *P. acuminatus* Zone. *g*, HM C13783, 0.7-0.85 m, *G. persculptus* Zone. *h*, HM C13904/1*a*, very long, apparently branching virgella, 1.56-1.66 m, *G. persculptus*/ *P. acuminatus* Zone. *i*, HM C13870/1*a*, long rhabdosome, 1.38-1.46 m, *G. persculptus* Zone.

and rounded proximal end and lacks the 'notch' formed by the exposed wall of the sicula in *C. normalis*. According to recent descriptions by Rickards (1970) and Hutt (1974) *C. rectangularis* is a much wider form than *C. normalis* with a maximum width of 2.0-2.5 mm, although the proximal end seems very similar to several specimens here assigned to *C. normalis* (e.g. text-fig. 4*e*). *C. rectangularis* has not been recorded earlier than the *A. atavus* or *C. vesiculosus* zones. *C. normalis* is separable from both *G. avitus* and *G. 'v. cf. venustus'* by its consistently 'box-like' thecae and it never displays the rather rounded supragenicular walls nor the forked virgella commonly seen in *G. avitus*.

C. normalis is also found in the *D. anceps* Zone at Dob's Linn (text-fig. 4c). It has been widely recorded from the top Ordovician and lower Silurian of north-west Europe (see synonymies), north-east Russia (Koren' *et al.* 1979, 1980), Greenland (Poulsen 1934), Morocco (Willefert 1963), North America (Churkin and Eberlein 1971; Riva and Petryk 1981), China (Hsü 1934), and Australia (Thomas 1960).

Climacograptus miserabilis Elles and Wood, 1906

Text-figs. 3f-i, ?j, 4f-i, 5a, b

- ?1895 *Diplograptus* (*Glyptograptus*) *euglyphus* Lapworth var. *angustus* mihi; Perner, p. 27, pl. 8, fig. 14a, b.
- ?1895 *Diplograptus* (*Glyptograptus*) *lobatus* n. sp.; Perner, p. 28, pl. 7, fig. 15; pl. 8, fig. 15.
- 1906 *Climacograptus scalaris* (Hisinger) var. *miserabilis* var. nov.; Elles and Wood, p. 186, pl. 26, fig. 3a-h; text-fig. 120a-c.
- ?1924 *Climacograptus miserabilis* Elles and Wood; Hundt, pl. 1, figs. 20, 21, 26.
- 1929 *Climacograptus scalaris* var. *miserabilis* Elles and Wood; Davies, p. 7 (*pars*), text-fig. 27.
- 1945 *Climacograptus scalaris* var. *miserabilis* Elles and Wood; Waterlot, pl. 4, fig. 91.
- 1949 *Climacograptus angustus* (Perner); Přibyl, p. 7, pl. 11, figs. 2-9.
- ?1963 *Climacograptus scalaris* var. *miserabilis*? Elles and Wood; Willefert, p. 14, pl. 3, figs. 12, 16; text-fig. 4.
- 1963 *Climacograptus angustus* (Perner); Skoglund, p. 40, pl. 3, figs. 1, 2, 4-6; pl. 4, fig. 7; pl. 5, fig. 6.
- 1965 *Climacograptus scalaris miserabilis* Elles and Wood; Stein, pl. 60, fig. 14f, h.
- 1970 *Climacograptus scalaris miserabilis* Elles and Wood; Toghill, p. 23, pl. 12, figs. 1-11.
- 1970 *Climacograptus miserabilis* Elles and Wood; Rickards, p. 28, pl. 1, figs. 3-5, 10.
- 1974 *Climacograptus miserabilis* Elles and Wood; Hutt, p. 20, pl. 1, figs. 1, 2; text-fig. 8, fig. 1.
- 1975 *Climacograptus angustus* (Perner); Bjerreskov, p. 23, text-fig. 9a.
- 1976 *Gl. (sic) (Climacograptus) miserabilis* Elles and Wood; Legrand, text-fig. 7.
- 1980 *Climacograptus angustus* (Perner); Koren' *et al.*, p. 131, pl. 37, figs. 2-7; text-fig. 34a-e.
- ?1980 *Climacograptus* aff. *angustus* (Perner); Koren' *et al.*, p. 132, text-fig. 35.

Type specimen. Not yet designated. Elles and Wood's material is from the Upper Hartfell Shale of Dob's Linn (mainly Lower Complanatus Band).

Material. Specimens in the Lapworth Collection (BU) used by Elles and Wood in their original description and numerous specimens, mostly flattened but some preserved in full relief, in my collections.

Horizons and localities. The basal 2.3 m of Birkhill Shale, *G. persculptus* and low *P. acuminatus* zones, Dob's Linn.

Diagnosis. Small rhabdosome up to 20 mm long, with a rapidly attained maximum width of 0.8 mm. Thecae may appear typically *Climacograptus* in style or possess slightly curved supragenicular walls, numbering nine to eleven in 10 mm. Long virgella and nema commonly present.

Description. The rhabdosome is only up to 20 mm long, widening from 0.5-0.7 mm at the aperture of $th1^1$ to the maximum 0.7-0.8 mm (1.0 mm in tectonically widened specimens) within 4 mm. Proximally the thecae number about eleven in 10 mm, reducing only slightly to nine to ten in 10 mm distally. The sicula is 1.0-1.3 mm long and is exposed for its entire length in obverse aspect. It possesses a conspicuous virgella which sometimes reaches over 10 mm long. $Th1^1$ grows initially down until it reaches the aperture of the sicula, then bends sharply upwards. $Th1^2$ appears to grow upwards for its entire length. When specimens are preserved in full biprofile orientation a slight proximal 'notch' is present where the sicula extends beyond $th1^2$, but the proximal end appears pointed when oriented obliquely. The median septum appears to commence on the reverse side opposite the aperture of $th1^2$ (below the apex of the sicula) and possesses an initial thickened node (text-fig. 3g). The remaining thecae may appear either typically *Climacograptus* in style with straight supragenicular walls and pronounced sharp genicula, or slightly *Glyptograptus*-like with rounded genicula and slightly convexly curved supragenicular walls, depending on the orientation of the rhabdosome. The apertures are normally slightly everted, opening into long excavations which occupy one-quarter the total width of the rhabdosome and are sub-alternate. The intertheal septa are slightly curved and short, extending only half the length of the supragenicular walls. A long nema is commonly present.

Remarks. The only coeval species with which *C. miserabilis* can be easily confused is *C. normalis* when tectonically widened. *C. miserabilis*, however, reaches its maximum width quickly as opposed to the more gradual widening of *C. normalis*, and even when tectonically stretched *C. miserabilis* rarely exceeds 1 mm wide. The proximal development and thecal style of *C. miserabilis* are also somewhat different with shorter intertheatal septa and commonly slightly curved supragenicular walls. Toghill (1970) recorded *C. miserabilis* from the *P. linearis* Zone, whilst Williams (1982a) shows that it is found as low as high *D. clingani* Zone in the Lower Hartfell Shale at Dob's Linn. Elles and Wood recorded the earlier small *Climacograptus*, *C. brevis* Elles and Wood, 1906 to be characteristic of the *N. gracilis* and *C. peltifer* zones with only rare specimens in the Lower Hartfell Shale.

The similarity of *C. miserabilis* to *C. angustus* (Perner, 1895) was first noted by Přibyl (1949, p. 7) who listed Elles and Wood's species as a junior synonym. Strachan (1971), however, pointed out that Perner's original specimen was a distal fragment and insufficient to erect as the type of a new species. Přibyl raised Perner's *G. euglyphus angustus* to full specific status, assigned it to *Climacograptus*, and synonymized *G. lobatus* which was described by Perner on the page following the description of *C. angustus*. It has since become apparent that the lower Silurian specimens of *C. miserabilis* match Perner's description of *C. angustus* more closely than the late Ordovician ones, which have a more typically *Climacograptus* thecal style (R. B. Rickards, pers. comm.). It is here considered that *C. miserabilis* is best retained as a separate species from *C. angustus* until further study of Perner's type and any topotype material is possible, although it is recognized that the lower Silurian specimens described here may be synonymous with Perner's material. It should be noted that *C. angustus* Sobolevskaya, 1969, a small *longispinus* group *Climacograptus* from the late Ordovician of the U.S.S.R., is a junior homonym of *C. angustus* (Perner, 1895) and should not be used.

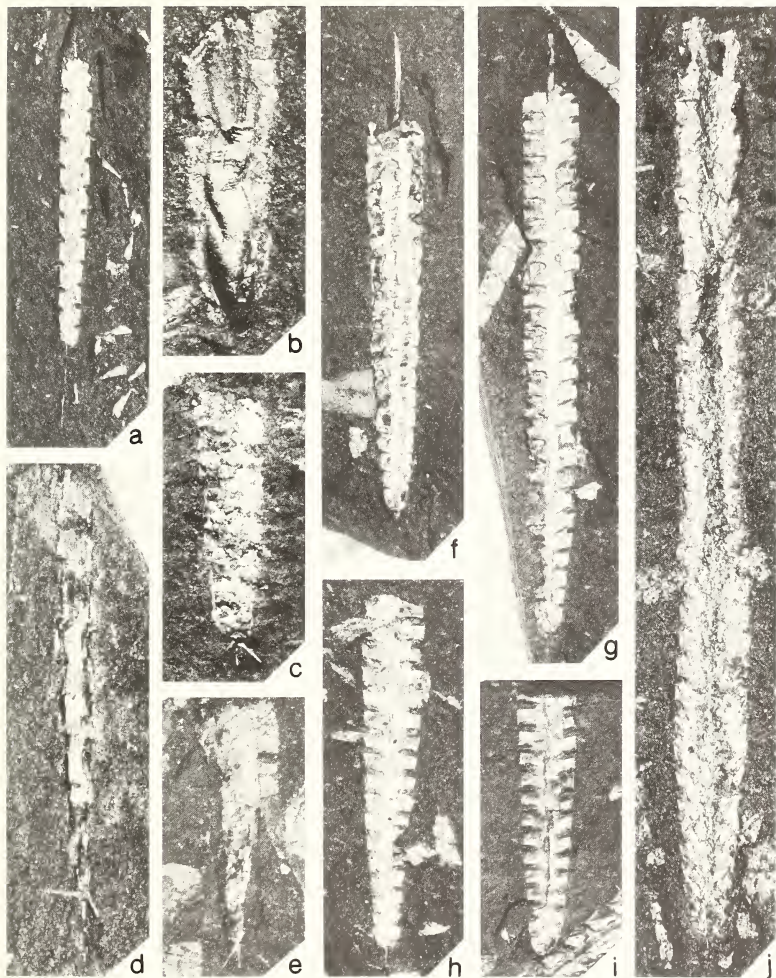
C. miserabilis is a widespread upper Ordovician and lower Silurian species, and if synonymized with *C. angustus* has been recorded from all equivalent graptolitic successions.

Climacograptus medius Törnquist, 1897

Text-fig. 5*f-i*

- 1870 *Climacograptus teretiusculus*; Nicholson (*pars*), p. 373, text-fig. 1*a, b, f* (non text-fig. 1*c-e*).
- 1872 *Climacograptus teretiusculus*; Nicholson (*pars*), p. 33, text-fig. 8*a, b, f* (non text-fig. 8*c-e*).
- 1873 *Climacograptus scalaris*; Malaise, p. 104, pl. 6, figs. 5-6.
- non 1837 *Prionotus scalaris*; Hisinger, p. 113, pl. 35, fig. 4.
- 1897 *Climacograptus medius* n. sp.; Törnquist, p. 7, pl. 1, figs. 9-15.
- 1906 *Climacograptus medius* Törnquist; Elles and Wood (*pars*), p. 189, pl. 26, fig. 4*a-e*; text-fig. 122*a, c* (non pl. 26, fig. 4*f*; text-fig. 122*b* = *C. trifilis* Manck, 1923).
- 1919 *Climacograptus medius* Törnquist; Kirste (*pars*), p. 107, pl. 1, fig. 4*b, 4a?* (non pl. 1, fig. 4*c, d*).
- ?1924 *Climacograptus medius* Törnquist; Hundt, pl. 1, figs. 22, 23, 35, 36.
- ?1929 *Climacograptus medius* Törnquist; Davies, text-fig. 32, fig. 4.
- 1933 *Climacograptus medius* Törnquist; Sun, p. 23, pl. 4, fig. 2.
- ?1940 *Climacograptus medius* Törnquist; Desio, p. 27, pl. 1, figs. 16, 17.
- 1945 *Climacograptus medius* Törnquist; Waterlot, pl. 6, fig. 113.

TEXT-FIG. 5. All except *j* from the Linn Branch trench, Dob's Linn. *a, b*, *Climacograptus miserabilis* Elles and Wood, 1906. *a*, HM C13862*a*, complete specimen with long virgella, 1.38-1.46 m, *G. persculptus* Zone, $\times 5$. *b*, HM C13909, reverse view, in partial relief; note growth fusellae and flattened exterior portions of thecae, 1.56-1.66 m, *G. persculptus*/*P. acuminatus* Zone, $\times 20$. *c*, *Climacograptus trifilis* Manck, 1923, HM C14020, 2.19-2.31 m, *P. acuminatus* Zone, $\times 10$. *d, e*, *Climacograptus* sp. (cf. *C. miserabilis*), with three basal spines as *C. trifilis*, but narrower, $\times 10$. *d*, HM C14027, 2.19-2.31 m, *P. acuminatus* Zone. *e*, HM C13978, 2.01-2.14 m, *P. acuminatus* Zone. *f-i*, *Climacograptus medius* Törnquist, 1897, $\times 5$. *f*, HM C13951, note median groove of wide nema, 1.88-2.0 m, *P. acuminatus* Zone. *g*, HM C13814, 1.1-1.2 m, *G. persculptus* Zone. *h*, HM C13888*a*, 1.46-1.56 m, *G. persculptus* Zone. *i*, HM C13916/1, 1.76-1.91 m, *P. acuminatus* Zone. *j*, *Climacograptus? extraordinarius* (Sobolevskaya, 1974), HM C13689, Anceps Band E, Upper Hartfell Shale, *P. pacificus* Subzone, Main Cliff section, Dob's Linn, $\times 5$.



- 1948 *Climacograptus medius* Törnquist; Waern, p. 449, pl. 25, fig. 4; text-fig. 5.
 ?1949 *Climacograptus medius* Törnquist; Obut, p. 13, pl. 1, fig. 3a, b.
 ?1957 *Climacograptus medius* Törnquist; Suter Coma, p. 49, text-fig. 1.
 1965 *Climacograptus medius* Törnquist; Stein, p. 163, text-fig. 16a-g, tables 7, 8.
 ?1970 *Climacograptus* cf. *C. medius* Törnquist; Churkin and Carter, p. 16, pl. 1, figs. 4, 5; text-fig. 6f.
 1970 *Climacograptus medius* Törnquist; Rickards, p. 30, pl. 1, fig. 2.
 1971 *Climacograptus medius* Törnquist subsp. indet.; Schauer, p. 31, pl. 2, figs. 1, 2; pl. 4, figs. 1-3.
 1974 *Climacograptus medius* Törnquist; Hutt, p. 19, pl. 1, fig. 3.
 1975 *Climacograptus medius* Törnquist; Bjerreskov, p. 24, text-fig. 9c.

Lectotype. The specimen figured by Törnquist (1897, pl. 1, fig. 9) from the Rastrites Beds of Nyhamn, Sweden. Designated by Přibyl (1948, p. 16).

Material. Fifteen flattened specimens and one in full relief, my collection.

Horizons and localities. From 1·1 to 2·3 m above the base of the Birkhill Shale, *G. persculptus* and low *P. acuminatus* zones, Linn Branch trench, Dob's Linn.

Diagnosis. Robust rhabdosome with a maximum width of 2·5 mm and wide rounded proximal end. Thecae with short straight supragenicular walls, numbering twelve or thirteen in 10 mm, excavations long and deep. Nema often broad.

Description. The rhabdosome is over 30 mm long, increasing from a width of 1 mm at the aperture of th1¹ to 1·7-1·9 mm in 5 mm and slowly reaching the maximum 2·2-2·5 mm within 15 mm. The thecae usually number thirteen in 10 mm proximally, reducing only slightly to twelve in 10 mm distally. The proximal development has not been observed in the described material. The sicula possesses a conspicuous but short virgella and the proximal region is wide and rounded. The thecae have short, straight supragenicular walls which are normally vertical but sometimes slightly inclined. The apertures are horizontal and open into very deep and long excavations which occupy one-third the total width of the rhabdosome and over one-third of the ventral walls. The excavations often appear deeper as the rhabdosome is commonly preserved in oblique orientation; the one specimen preserved in full relief shows that this is due to the almost circular cross-section of the rhabdosome. The virgula is normally extended as a long and wide nema, which may have been cylindrical owing to the median groove that is commonly present.

Remarks. *C. medius* is the most robust *Climacograptus* species found in the *P. acuminatus* Zone of Britain. It could be confused with tectonically widened specimens of *C. normalis* but this never attains the maximum width of *C. medius*. *C. medius* seems closest to *C. trifilis* Manck, 1923 which has a similar-sized rhabdosome, but the sicula of this species possesses three spines and the rhabdosome widens more rapidly to a rather narrower maximum width. *C. medius* is more robust proximally than *C. rectangularis* which is only 0·7 mm wide at the aperture of th1¹. *C. medius* has sometimes been recorded as occurring rarely in the *P. acuminatus* Zone but with its main development in the *A. atavus* to *M. triangularis* zones (Rickards 1970; Hutt 1974), although Stein (1965), Toghil (1968b), and Rickards (1976a, b) record the range as *G. persculptus* to *C. cyphus* zones.

C. medius has been recorded from the lower Silurian of Europe, Morocco (Waterlot 1945), China (Sun 1933), U.S.S.R. (Obut and Sobolevskaya 1966), and questionably from North America (Churkin and Carter 1970).

Climacograptus trifilis Manck, 1923

Text-fig. 5c

- 1906 *Climacograptus medius* Törnquist; Elles and Wood (*pars*), p. 189, pl. 26, fig. 4f; text-fig. 122b (*non* pl. 26, fig. 4a-e; text-fig. 122a, c = *C. medius* s.s.).
 1923 *Climacograptus trifilis* spec. nov. Manck, p. 288, text-fig. 32.
 1965 *Climacograptus trifilis* Manck; Stein, p. 165, text-fig. 17a-d [see also for full synonymy list].
 1975 *Climacograptus trifilis trifilis* Manck; Bjerreskov, p. 23, text-fig. 9b.

Holotype. The specimen figured by Manck (1923, text-fig. 32) from an unknown locality and horizon.

Material. One flattened specimen in my collection.

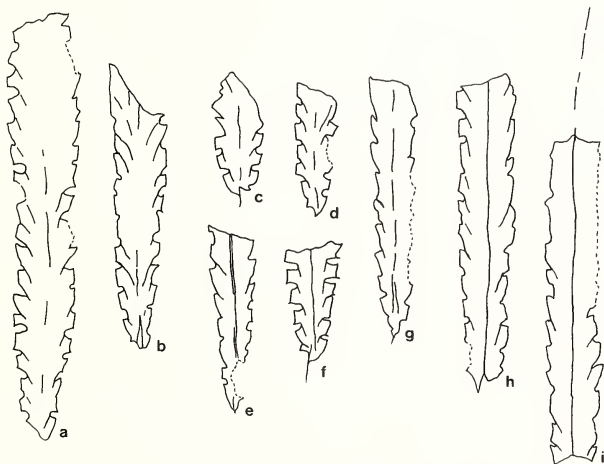
Horizons and localities. The interval 2.2 to 2.3 m above the base of the Birkhill Shale, low *P. acuminatus* Zone, Linn Branch trench, Dob's Linn.

Remarks. This species was described in detail by Stein (1965). It has a similarly robust proximal end to *C. medius* but is distinguished by the presence of three proximal spines, apparently derived from a point near the origin of the virgella. From Stein's description *C. trifilis* appears to be commonly preserved in scalariform and oblique orientation and therefore probably had a similar cylindrical cross-section to *C. medius*. From the records by Stein (1965, p. 167), Toghil (1968*b*, p. 658), and Bjerreskov (1975, p. 23) *C. trifilis* appears to be restricted to the *P. acuminatus* Zone and it has not been recorded outside Europe.

Climacograptus? extraordinarius (Sobolevskaya, 1974)

Text-figs. 5*j*, 6*a-i*, 7*a-c*

- 1974 *Fenhsiangograptus extraordinarius* sp. nov.; Sobolevskaya, p. 69, pl. 3, figs. 6, 7.
 ?1974 *Diplograptus orientalis* sp. nov.; Mu *et al.*, p. 213, pl. 98, fig. 11.
 ?1978 *Diplograptus orientalis* Mu *et al.*; Wang and Zhao, p. 641, pl. 207, fig. 6 [same specimen as illustrated by Mu *et al.* 1974].
 1979 *Climacograptus? extraordinarius* (Sobolevskaya); Rickards, text-fig. 2.
 ?1980 *Glyptograptus? persculptus* (Salter) forma A; Koren' *et al.*, p. 147, pl. 42, figs. 3-6; pl. 43, fig. 1; pl. 44, figs. 1-6; text-fig. 44*a-j*.



TEXT-FIG. 6. *Climacograptus? extraordinarius* (Sobolevskaya, 1974). *Extraordinarius* Band, Upper Hartfell Shale, *C? extraordinarius* Zone, Long Burn trench, Dob's Linn, Ingham collection, all $\times 5$. *a*, HM C14479/33, distal fragment. *b*, HM C14479/45, proximal fragment in obverse view showing sicula and proximal development. *c*, HM C14479/1, proximal fragment with prominent virgella and 'notch' below th1². *d*, HM C14479/22. *e*, HM C14479/21. *f*, HM C14479/16, proximal fragment with clear proximal structure. *g*, HM C14479/5, proximal fragment with sicula faintly visible. *h*, HM C14479/25, distal fragment. *i*, HM C14479/23, distal fragment with free nema.

Holotype. Specimen No. 602x/1 figured by Sobolevskaya (1974, pl. 3, fig. 6).

Material. About fifty specimens in the Ingham Collection (HM) and six specimens in my collection (all flattened).

Horizons and localities. Extraordinarius Band, Upper Hartfell Shale, *C?* *extraordinarius* Zone, Long Burn and Main Cliff sections, Dob's Linn. Anceps Band E, Upper Hartfell Shale, *P. pacificus* Subzone, Main Cliff section, Dob's Linn.

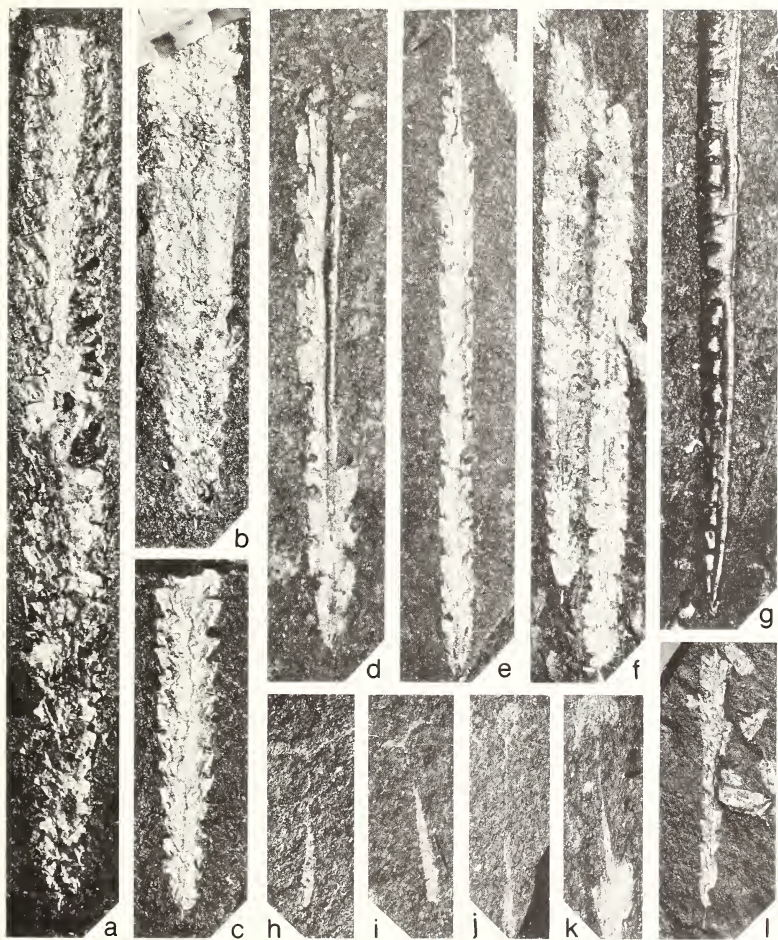
Diagnosis. Rhabdosome over 35 mm long, rapidly widening to the maximum 2.5–3.0 mm. Distally somewhat fusiform. Thecae intermediate between *Glyptograptus* and *Climacograptus*, numbering ten to twelve in 10 mm. Sicula with prominent virgella, anti-virgellar side forms conspicuous 'notch' under $th1^2$.

Description. The rhabdosome is up to 35 mm long with a robust, sub-fusiform outline, widening rapidly from 1.0–1.2 mm at the aperture of $th1^1$ to the maximum 2.3–3.0 mm within 8 mm and commonly decreasing in width soon after. Proximally the thecae number twelve in 10 mm, reducing distally to ten in 10 mm. The sicula is rarely seen but possesses a conspicuous virgella up to 1 mm long. $Th1^1$ grows downwards initially until it reaches a level about 0.3 mm below the aperture of the sicula, then bends abruptly upwards to give an aperture about 0.9 mm above its lowest point. $Th1^2$ appears to grow upwards throughout its length, cutting diagonally across the sicula some 0.3 mm above its aperture and resulting in a 'notch' where the anti-virgellar side of the sicula remains exposed. The remaining thecae are highly variable in style due to diagenetic flattening in a variety of orientations and to tectonic deformation. When relatively undeformed biprofile orientations are seen, the thecae have short, straight, gently inclined supragenicular walls with conspicuous genicular flanges. The apertural excavations are long, occupying over one-third of the total ventral wall, but are shallow, commonly occupying only one-fifth to one-sixth of the total rhabdosome width. The intertheatal septa are almost straight. The virgula is commonly pressed through the periderm and visible throughout the rhabdosome; it occasionally extends distally as a free nema up to 5 mm long. It is unclear whether a median septum exists, although by comparison with other similar diplograptids this is likely to be present.

Remarks. The proximal development of the specimens here assigned to *C?* *extraordinarius* is very similar to that found in *Glyptograptus persculptus* and they are evidently closely related. The main differences between the two species are the prominent genicular flanges and distal narrowing of *C?* *extraordinarius*. It is possible that some of the specimens figured here as *C?* *extraordinarius* are actually deformed specimens of *G. persculptus* s.l., as the tectonic deformation present at Dob's Linn, particularly in the Extraordinarius Band where it is more extreme, may alter the thecal style drastically, and subtle differences may not be recognized reliably.

The dimensions and thecal counts (when deformation is accounted for) agree well with Sobolevskaya's original (1974) description and figures. The remaining specimens from the Ingham Collection figured by Rickards (1979, text-fig. 2) have consistently more vertical supragenicular walls but are otherwise similar to those described here. The three-dimensional specimens of *G. persculptus*

TEXT-FIG. 7. *a–c*, *Climacograptus? extraordinarius* (Sobolevskaya, 1974). Anceps Band E, Upper Hartfell Shale, *P. pacificus* Subzone, Main Cliff section, Dob's Linn, $\times 5$. *a*, HM C13709. *b*, HM C13705. *c*, HM C13690. *d–f*, *Glyptograptus? 'venustus' cf. venustus* (Legrand, 1976). Basal 0.46 m, *G. persculptus* Zone, Linn Branch trench, Dob's Linn. *d*, HM C13738/1, with uniserial distal portion, possibly due to post-mortem breakage in this specimen (also figured text-fig. 8*h*), $\times 10$. *e*, HM C13747/1, almost complete rhabdosome (also figured text-fig. 8*d*), $\times 5$. *f*, HM C13747/2–3, tectonically widened rhabdosomes (also figured text-fig. 8*a*), $\times 5$. *g*, *Climacograptus normalis* Lapworth, 1877, HM C13972, external mould, in relief, oblique orientation, 1.88–2.0 m, *P. acuminatus* Zone, Linn Branch trench, Dob's Linn, $\times 5$. *h–l*, *Glyptograptus? avitus* Davies, 1929. *h–k*, *G. persculptus* Zone, Linn Branch trench, Dob's Linn, $\times 10$. *h*, HM C13837, sicula with 'lime seed vane'-like structure, 1.2–1.32 m. *i*, HM C13840, as *h*, 1.2–1.32. *j*, HM C13815, sicula with 'disc'-like structure, 1.1–1.2 m. *k*, HM C13882, juvenile with first two thecae and biconcavo-convex structure, 1.46–1.56 m. *l*, SM A10019, Holotype, note specimen is tectonically stretched, giving a more slender appearance than is normal for this species; from the low Birkhill Shale (labelled '*acuminatus*' Zone but may actually be from the *persculptus* Zone—see comments in text), Dob's Linn; figured Davies (1929, text-fig. 21), Packham (1962, text-fig. 7*a*), $\times 5$.



forma A described by Koren' *et al.* (1980) appear similar to *C? extraordinarius* proximally but they do not figure any complete specimens. Only the holotype of *D. orientalis* has been figured; it has prominent genicular flanges on the early thecae and a sub-fusiform outline very similar to *C? extraordinarius*, and Enzhi Mu (pers. comm.) considers that the two species may be synonymous. *Diplograptus multidentis orientalis* Wang *et al.*, 1977 is from an earlier horizon containing *Dicranograptus ramosus longicaulis* Elles and Wood, 1904 and *Dicranograptus clingani* Carruthers, 1868, and should not be confused with the late Ordovician *D. orientalis*.

C? extraordinarius is now used as a late Ordovician zone fossil in both Russia and Scotland, although this study shows it to range from high *P. pacificus* Subzone at Dob's Linn. If *D. orientalis* from the top Ordovician *D. bohemicus* Zone of central China is synonymous with *C? extraordinarius* it would appear to be a fairly widespread species and even more useful for correlation than presently recognized.

Genus GLYPTOGRAPTUS (GLYPTOGRAPTUS) Lapworth, 1873

Type species (by original designation). *Diplograptus tamariscus* Nicholson, 1868, p. 526, pl. 19, figs. 10–13.

Diagnosis (after Bulman 1970, p. V126). Thecae alternate with gentle sigmoidal curvature, supragenicular walls normally slightly convex, sometimes with slight genicula.

Glyptograptus persculptus (Salter, 1865)

Plate 66, figs. 1–3

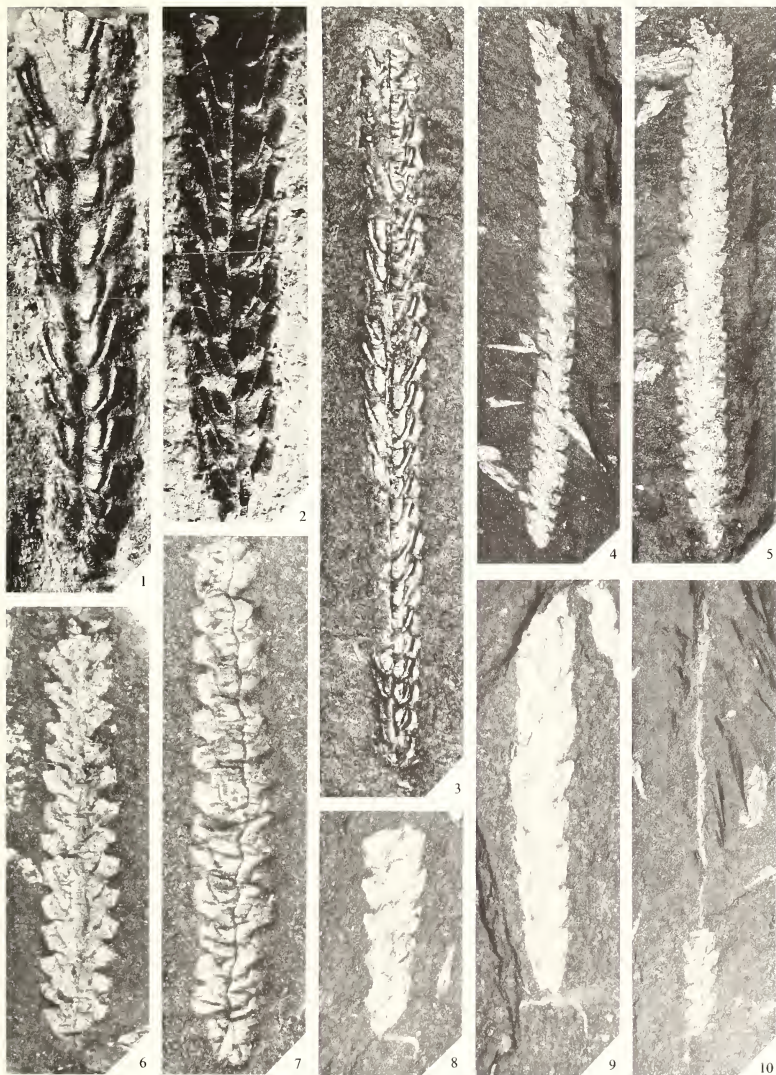
- 1865 *Diplograptus persculptus* [Salter?]; Salter, p. 25 (see Strachan 1971).
- 1868 *Diplograptus persculptus*; Carruthers, p. 130.
- 1878 *Diplograptus persculptus* Salter; Salter, p. 23.
- 1907 *Diplograptus* (*Glyptograptus*) *persculptus* Salter; Elles and Wood, p. 257, pl. 31, fig. 7a–c; text-fig. 176a, b.
- 1929 *Glyptograptus* aff. *persculptus* Salter; Davies, p. 10, text-fig. 11a.
- 1929 *Glyptograptus persculptus* mut.; Davies (*pars*), p. 11, text-figs. 11, 13, 15–18 (*non* text-figs. 12, 14, 19 = *G. cf. persculptus sensu* this paper).
- 1929 *Glyptograptus persculptus* mut. *omega* nov.; Davies, text-figs. 15, 20.
- 1977 *Glyptograptus persculptus* (Salter); Rickards *et al.*, p. 99, pl. 2, fig. 4; text-figs. 8, 53.

Lectotype (here designated). GSM 11782, the only well-preserved specimen in Salter's collection; from Ogofau, Pumpsaint, mid Wales; figured Pl. 66, fig. 3.

Material. Salter's specimens (I.G.S. collections, South Kensington), two specimens illustrated by Elles and Wood (collections of the BM) and material in the Davies Collection (SM).

EXPLANATION OF PLATE 66

- Figs. 1–3. *Glyptograptus persculptus* (Salter, 1865) *sensu stricto*. Basal Silurian(?), *G. persculptus*/*P. acuminatus* Zones, Ogofau, Pumpsaint, Dyfed, mid Wales. 1, BM Q112, obverse view in full relief, with apparently complete scula, (?)figured Elles and Wood (1907, text-fig. 176a), $\times 10$. 2, BM Q113, broad specimen with broken proximal end, in partial relief, figured Elles and Wood (1907, text-fig. 176b, with complete proximal end), $\times 10$. 3, GSM 11782, proposed lectotype, the only well-preserved specimen collected by Salter, $\times 5$.
- Figs. 4–7. *Glyptograptus* cf. *persculptus* (Salter, 1865). Linn Branch trench, Dob's Linn. 4, HM C14023/1a, 2.19–2.31 m, *P. acuminatus* Zone, $\times 5$. 5, HM C13848a, 1.2–1.32 m, *G. persculptus* Zone, $\times 5$. 6, HM C13963, 1.88–2.0 m, *P. acuminatus* Zone, $\times 10$. 7, HM C13965a, obverse view in partial relief, 1.88–2.0 m, *P. acuminatus* Zone, $\times 10$.
- Figs. 8–10. *Glyptograptus? avitus* Davies, 1929. *G. persculptus* Zone, Linn Branch trench, Dob's Linn. 8, HM C13906/1, 1.56–1.66 m, $\times 10$. 9, HM C13895, 1.56–1.66 m, $\times 10$. 10, HM C13806, distal fragment with membranous nema, 1.1–1.2 m, $\times 5$.



Horizons and localities. Zones of *G. persculptus* and *P. acuminatus*, gold mines at Ogofau, Pumpsaint, Dyfed, and other localities in mid Wales.

Diagnosis. Large rhabdosome up to 30 mm long and 2–3 mm wide with sigmoidally curved thecae and wavy median septum. Thecae with curved supragenicular walls and slightly everted apertures, numbering nine to eleven in 10 mm.

Description. The rhabdosome is up to 30 mm long, widening from about 1 mm at the aperture of $Th1^1$ to 1.5–1.7 mm in 5 mm and slowly reaching the maximum 2.0–2.7 mm in 15 mm which is then maintained. Proximally the thecae number ten to eleven in 10 mm, decreasing distally to nine in 10 mm. The sicula is revealed for 1.2 mm in obverse view; Elles and Wood recorded the sicula to be 2.1 mm long when observed in juvenile specimens, although Davies's serial sections (1929, text-fig. 11a) indicated that the sicula is only 1.2 mm long and obversely exposed for its entire length. $Th1^1$ grows down until it is about 0.15 mm below the aperture of the sicula before bending abruptly upwards. $Th1^2$ apparently grows upwards for its entire length, giving the proximal region a distinctive, asymmetrical appearance. The remaining thecae are sigmoidally curved and possess slightly everted apertures which open into narrow excavations occupying only about one-sixth of the total rhabdosome width. The supragenicular walls are gently convex, with slight genicula which become more pronounced when the rhabdosome is oriented obliquely. The thecae remain alternate throughout the rhabdosome, resulting in a gently sinuous median septum which is complete in obverse view, although Davies (1929) considered that the median septum appeared later on the reverse side higher up the succession. Neither virgella nor distally free nema have been observed on any specimens.

Remarks. The classification of *G. persculptus* is confused owing to its origin as an undescribed *nomen nudum*. Fortunately, the material described by Elles and Wood (1907) appears to be identical with Salter's specimens and it is proposed that their description should be taken as the type one. It does, however, contain some internal discrepancies both within the text (e.g. the diagnosis lists the thecae as 2 mm long, while the description records them as 3 mm) and with the illustrations, so care must be taken when using it. If Elles and Wood's description is accepted as the type it could be argued either that because the name is a certain *nomen nudum* it should be dropped, or that Elles and Wood should become the authors of the species. As *G. persculptus* is such a well-established species in international literature it would not be wise to change the name. Elles and Wood apparently had access to Salter's material in addition to their own and obviously considered it to be his species; it is therefore considered justifiable to retain Salter as the author of *G. persculptus* in the cause of nomenclatorial stability, although he never described or illustrated it.

It appears that many specimens identified as *G. persculptus* are not strictly referable to this species and that the name is now applied to a variety of diplograptids which possibly belong to several different genera. It is suggested here that the name should be used only for specimens strictly comparable with the type material from Pumpsaint. Difficulty arises when comparing flattened specimens with the type material, which is preserved in relief, but an indication of the expected appearances can be seen by comparing specimens of *G. cf. persculptus* from Dob's Linn (Pl. 66, figs. 4–7) which are preserved both flattened and in relief. Davies (1929, p. 14) and Rickards (1976a, p. 158) pointed out that *G. persculptus* and *Diplograptus m. modestus* Lapworth, 1876 may be easily confused when flattened and that caution should be exercised when using faunal lists containing both names.

Davies's specimens (1929, text-figs. 14, 19 and unfigured material in the Sedgwick Museum) of '*G. persculptus* mut.' and Hutt's specimens of '*G. persculptus*' (1974, pl. 6, figs. 9–12), all from the English Lake District, are similar but rather smaller than the type material and are here referred to *G. cf. persculptus*, as is Davies's figured specimen of '*G. persculptus* mut.' from Dob's Linn (1929, text-fig. 12). This latter form is rather less robust and has a poorly developed periderm, giving far less contrast with the surrounding lithology than other associated diplograptids, as opposed to the well thickened one of *G. persculptus s.s.* Davies (1929, p. 14) seems to have been aware of this variation; he stated that specimens of *G. persculptus* from the Moffat area were, on the whole, smaller than those in Wales whilst those in the Lake District were intermediate between the two. The specimens of '*G. persculptus*' described by Bjerreskov (1975) from Bornholm have a fairly narrow rhabdosome (maximum 1.6 mm in relief, 2.0 mm flattened) but a low thecal count (ten in 10 mm) and it is unclear whether they may be assigned to *G. persculptus s.s.*

Although it would be necessary to see the specimens before stating anything conclusively, none of the specimens figured by Koren' *et al.* (1980) as *G. persculptus* forma A and forma B appears to me to belong to *G. persculptus* s.s. Their forma A has more pronounced genicula, straighter supragenicular walls, widens more rapidly, and appears to narrow distally; it is possibly synonymous with *Climacograptus? extraordinarius* as, according to their range chart, it is restricted to the base of the *G. persculptus* Zone. Forma B has a far narrower form and straighter supragenicular walls, interthecal septa, and median septum than *G. persculptus* s.s. Churkin *et al.* (1971) recorded *G. persculptus* from the lowest Silurian of Alaska but did not describe or figure any material.

Glyptograptus cf. *persculptus* (Salter, 1865)

Plate 66, figs. 4-7

- 1929 *Glyptograptus persculptus* mut.; Davies (*pars*), p. 11, text-figs. 12, 14, 19 (*non* text-figs. 11, 13, 16-18 = *G. persculptus* s.s.).
 1974 *Glyptograptus persculptus* (Salter); Hutt, p. 28, pl. 6, figs. 9-12.

Material. Specimens in the Davies and Hutt collections (SM) and many specimens in my collections, including several preserved in partial relief.

Horizons and localities. From 0.7 to 2.3 m above the base of the Birkhill Shale, *G. persculptus* and low *P. acuminatus* zones, Linn Branch trench, Dob's Linn. Davies's and Hutt's material mostly from the Skelgill Beds, *G. persculptus* and *P. acuminatus* zones, Torver Beck and Yewdale Beck, Coniston, northern England. One of Davies's specimens (1929, text-fig. 12) from the Birkhill Shale, Dob's Linn.

Diagnosis. Similar to *G. persculptus* s.s. but with a smaller rhabdosome up to 20 mm long and 1.7 mm wide. Thecae number eleven to seventeen in 10 mm in tectonically distorted specimens.

Description. The rhabdosome is up to 20 mm long, widening rapidly from 1 mm at the aperture of th¹ to a maximum of 1.5-1.7 mm within 5 mm (undistorted). Proximally the thecae number fourteen to seventeen in 10 mm, reducing distally to eleven to thirteen in 10 mm. Only one specimen (Pl. 66, fig. 7) preserved in oblique view shows a sicula, which is visible for 0.8 mm. A short virgella is commonly visible in well-preserved material. The proximal development is obscure in the described specimens but appears similar to *G. persculptus* s.s. The remaining thecae have a similar style to *G. persculptus* s.s., normally possessing curved supragenicular walls, although these may appear straight or have slight geniculation depending on the orientation of the rhabdosome. The thecae are alternate throughout, although oblique tectonic deformation sometimes causes them to appear opposite. A distally free nema has only been observed on one specimen.

Remarks. This material is broadly comparable with *G. persculptus* s.s. but differs from the type specimens in having a smaller and narrower rhabdosome, a higher thecal count, and a less well-developed periderm. The specimens from Dob's Linn agree well with those described as *G. persculptus* by Hutt (1974) from the Skelgill Beds of the Lake District, which Rickards (1976a, p. 157) and Rickards *et al.* (1977) recognized as being smaller than the type material. Rickards (1976a), however, stated that much variation occurred in specimens from the Lake District and Dob's Linn, concluding that there were probably several subspecies involved. *G. cf. persculptus* may only be confused with *G? v. cf. venustus* in the collections from Dob's Linn, but differs from this by its less well-developed periderm, thecal style, and lack of a long virgella or nema. The present work indicates clearly that *G. cf. persculptus* occurs, albeit rarely, in the low *P. acuminatus* Zone, supporting the range given by Toghil (1968b) for '*G. persculptus*'.

Glyptograptus? avitus Davies, 1929

Plate 66, figs. 8-10; text-figs. 7h-l, 9a-c, ?d, 10a-c

- 1929 *Glyptograptus(?) avitus* sp. nov.; Davies, p. 8, text-fig. 21.
 1962 *Glyptograptus(?) avitus* Davies; Packham, text-fig. 7a.
 1965 *Glyptograptus(?) avitus* Davies; Stein, p. 172, text-fig. 22g.

Holotype. SM A10019, the specimen figured by Davies (1929), Packham (1962), and in this paper as text-fig. 7*h*; from the Birkhill Shale (*P. acuminatus* Zone?—see *Remarks*), Dob's Linn.

Material. The holotype and numerous flattened fragmentary specimens in my collections.

Horizons and localities. From 0.7 to 1.6 m above the base of the Birkhill Shale, *G. persculptus* Zone, Linn Branch trench, Dob's Linn.

Diagnosis. Small rhabdosome, increasing rapidly from 0.8 to 1.2 mm wide in 5 mm then slowly to 1.5 mm maximum. Thecae with slightly curved or straight, sloping supragenicular walls. Virgella commonly bifurcating, nema often with irregular, apparently membranous, structures.

Description. The longest fragment in the material described here is 8 mm long. The rhabdosome is 0.8–0.9 mm wide at the aperture of *th*¹ and increases to 1.2 mm in 5 mm. Davies (1929) recorded the rhabdosome to then widen slowly throughout its length to a distal maximum of 1.5 mm. The thecae number about twelve in 10 mm proximally, reducing to about ten in 10 mm distally. The sicula is approximately 2 mm long; it possesses a virgella which bifurcates after 1 to 4 mm and occasionally forks a second time (text-fig. 9*b*). The nemata of siculae in association with, and apparently belonging to, *G? avitus* characteristically possess distal structures, taking the form of a double concavo-convex or 'disc'-shaped vane-like structure (text-fig. 7*h–k*). *Th*¹ appears to grow down below the level of the sicula before bending up whilst *th*² grows continuously upwards, in a similar fashion to *G. persculptus*. The later thecae have slightly curved or straight, sloping supragenicular walls, although occasionally a slight geniculum is present. The preservation is insufficient to allow determination of the internal structure, but the outline with alternate thecae does suggest an affinity with *Glyptograptus*. A long, distally free nema is usually present; in juvenile specimens it commonly bears a vane-like structure at the distal extremity (see above) whilst more mature specimens often possess apparently membranous structures at various points along its length. (Pl. 66, fig. 10, text-figs. 9*c*, 10*b*).

Remarks. The holotype has been tectonically stretched longitudinally. The specimens described here agree well with Davies's description except that he did not record any specimens with forked virgellae. *G? avitus* is distinguished from other coexisting species by its thecal style, which is closest to the earlier *G. 'v. cf. venustus'*. Davies recorded *G? avitus* to be characteristic of the *G. persculptus* Zone (1929, p. 22, text-fig. 32), but in his description of the holotype (1929, text-fig. 21) recorded it to originate from the '*A. acuminatus* Zone'. Unfortunately, he gave no reference to the range of the species in the description other than 'L. Birkhill Shale'. The type slab contains no other zonally diagnostic faunal elements. The present study suggests that *G? avitus* is restricted to the *G. persculptus* Zone at Dob's Linn and that the label on the holotype must therefore be incorrect. Stein (1965), however, recorded *G? avitus* (with a forked virgella) from the *P. acuminatus* Zone of the Frankenvald, and Rickards (1976*a*) stated that he had identified the species from the *P. acuminatus* Zone at Conwy, north Wales.

In his original description Davies suggested that *G? avitus* was a 'forerunner' of *Akidograptus ascensus* Davies, 1929; I consider that there is insufficient evidence to demonstrate an evolutionary link between the two as implied by Davies. The membranous features attached distally to the nemata of siculae and juvenile rhabdosomes of *G? avitus* may have been vane-like structures to facilitate dispersal. The only structures in coeval diplograptids similar to those associated with the nemata of mature rhabdosomes of *G? avitus* were described by Müller (1977, pl. 4, figs. 1–7), who referred his specimens to *Climacograptus* sp. and *Diplograptus* cf. *modestus*. None of his specimens is considered here to belong to *G? avitus*. Müller (1975, 1977) considered the *P. acuminatus* Zone to represent an interval with diplograptids showing 'ramose' type (bifurcating) virgellae, although *G? avitus* is restricted to the *G. persculptus* Zone at Dob's Linn. The specimen referred to '*G. aff. avitus*' by Koren' *et al.* (1980, p. 140, text-fig. 41) is much narrower than *G? avitus* and has more steeply inclined supragenicular walls.

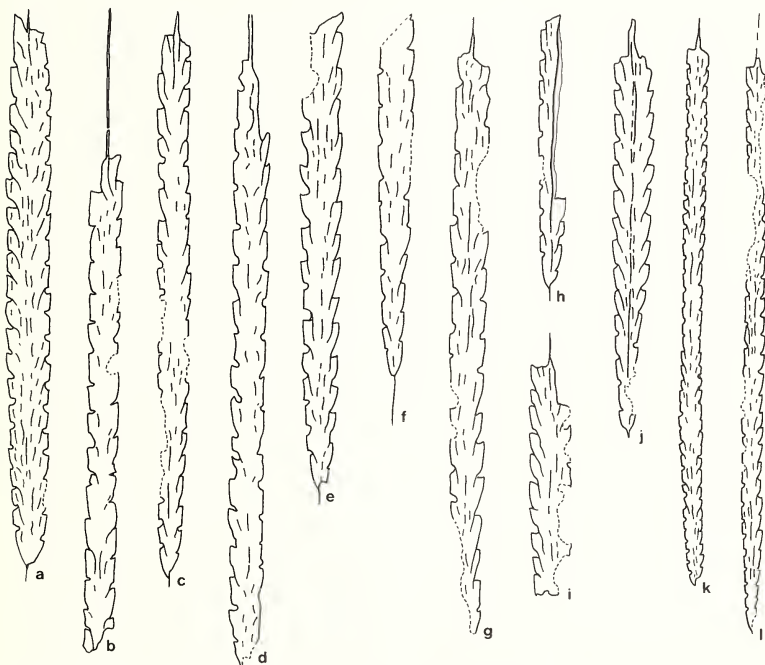
Glyptograptus? 'venustus' cf. venustus (Legrand, 1976)

Text-figs. 7*d–f*, 8*a–l*

non 1959 *Climacograptus venustus* sp. nov.; Hsü, p. 349, pl. 1, figs. 1–6, 13.

- cf. 1976 *Cl. (Climacograptus) venustus venustus* nov. subsp.; Legrand, p. 158, text-fig. 3a-e, table 3.
 1976 ?*Cl. (Climacograptus) venustus venustus* nov. subsp.; Legrand, text-fig. 4a.
 1976 *Cl. (Climacograptus)* cf. *normalis* Lapworth; Legrand (*pars*), text-fig. 4b (*non* text-fig. 4c = *C. normalis*?).
 non 1976 ?*Climacograptus (Climacograptus) venustus venustus* nov. subsp.; Legrand, p. 164, text-fig. 5a, b.
 ?1976 *Climacograptus (Climacograptus) venustus venustus* (*sic* = *venustus venustus*) nov. subsp.; Legrand, p. 166, text-fig. 6.

Note. This species group is about to be renamed by Legrand (*in press*) to avoid confusion with Hsü's (1959) previously described species.



TEXT-FIG. 8. *Glyptograptus?* 'venustus cf. venustus' (Legrand, 1976). Basal 0.46 m, *G. persculptus* Zone, Linn Branch trench, Dob's Linn, all $\times 5$ except figs. k, l. a, HM C13747/2, complete, tectonically widened specimen (also figured text-fig. 7f). b, HM C13729/2, distal fragment with long nema. c, HM C13738/2, complete specimen with characteristic proximal thickening at base of nema. d, HM C13747/1, almost complete specimen with short uniserial distal portion (also figured text-fig. 7e). e, HM C13722, specimen showing proximal 'notch' below th¹ and typical thecal style. f, HM C13747/5, proximal fragment with long virgella. g, HM C13747/6, distal fragment. h, HM C13738/1, small rhabdosome with long uniserial portion, possibly broken (also figured text-fig. 7d). i, HM C13747/4, distal fragment with short uniserial portion. j, HM C13747/7, complete specimen with thickened nema. k, HM C13729/1, long complete rhabdosome, $\times 2.5$. l, HM C13747/8, long complete rhabdosome, $\times 2.5$.

Material. Over thirty flattened specimens in my collections.

Horizons and localities. From 0.2 to 0.46 m above the base of the Birkhill Shale, *G. persculptus* Zone, Linn Branch trench, Dob's Linn.

Description. The rhabdosome is up to 40 mm long. It measures 0.8–1.1 mm (0.9 mm undeformed) wide at the aperture of th^1 , widening to 1.2–1.5 mm in 5 mm (1.3 mm undistorted) and reaching the maximum 1.2–1.8 mm (1.5 mm undistorted) in 12 mm. The thecae proximally number ten to twelve in 10 mm (undistorted), reducing distally to eight to ten in 10 mm. The proximal development is unclear, although th^1 extends some 0.2 mm below the aperture of the sicula before turning up and the proximal end is fairly pointed. Most specimens possess a conspicuous virgella up to 2.5 mm long. The thecae appear intermediate between *Climacograptus* and *Glyptograptus*; the supragenicular walls are inclined to an extent and may be either curved or straight with a sharp geniculum, depending on the orientation of the rhabdosome and relative direction of tectonic stretching. The apertures are normally horizontal or slightly introverted and open into excavations occupying one-quarter to one-fifth the total rhabdosome width. The stipe often becomes uniserial distally, one specimen having a uniserial portion 13 mm long, although this interval is normally shorter. This uniserial development commonly appears to be an astogenetic mutation rather than a post-mortem preservational feature (although this does occur, e.g. text-fig. 7d) and is too random to be a normal growth development. A nema often reaching several millimetres long is commonly present.

Remarks. This material from the lowest Birkhill Shale has been strongly affected by tectonic distortion, making quantitative measurements unreliable. The specimens described here are slightly longer with shorter virgellae than the type material of *G?* '*v. venustus*', but otherwise agree well both in thecal style and overall form. In his original description Legrand (1976) stated that the main difference between '*C. v. venustus*' and '*C. venustus venustus*' (misspelt in the original title as '*C. venustus venustus*') was the smaller overall form of the latter subspecies. This criterion would seem unreliable; however, he recorded '*C. venustus venustus*' to be restricted to the lowest part of the 'Silurian' succession in the Algerian Sahara whilst '*C. v. venustus*' had a far longer range. It is therefore possible that they are true stratigraphical subspecies.

One of the specimens figured by Legrand (1976, text-fig. 4b) as '*C. cf. normalis*' from the *G. persculptus* Zone of Dob's Linn is evidently identical to those specimens described here, as is the specimen of '*C. v. venustus*' from the Sahara figured by him (1976, text-fig. 4a). His specimen in text-fig. 4c is, however, closer to *C. normalis* s.s. The material described by Legrand (1976, p. 164, text-fig. 5a, b) as '*C. v. venustus*' is closer to *C. normalis* in thecal style and overall form but has much larger, *Amplexograptus*-like thecal excavations. '*C. venustus* nov. subsp. A' described by Legrand (1976, p. 169, text-fig. 8) has a much narrower, shorter rhabdosome than *G?* '*v. venustus*' and is restricted to a higher part of the succession.

The members of the *G?* '*venustus*' group are clearly distinct from *G. persculptus* s.s. in their general form, thecal style, and prominent virgella and nema. Their generic position is uncertain but they are here assigned questionably to *Glyptograptus* because of the slight curvature of the supragenicular walls and the lack of well-developed genicular hoods. The thecal style, lower thecal count, and thicker periderm readily separates them from *G. cf. persculptus*. The overall form is similar to *C. normalis* but the thecae of that species have consistently vertical supragenicular walls, conspicuous genicula, and horizontal apertures. I therefore consider that Riva (1981, p. 297) is incorrect in stating that 'there is no clearcut morphological criterion separating these two taxa [*C. normalis* and '*C. v. venustus*'] besides relative width and a longer virgella in the Sahara specimens. A lumping paleontologist might be tempted to expand the diagnosis of *C. normalis* to include *C. venustus venustus*.'

G? '*v. cf. venustus*' is similar to *G. persculptus* forma B of Koren' *et al.* (1980) in both form and stratigraphical range, but the latter taxon has more steeply inclined supragenicular walls, is generally wider, and does not show the tendency to develop a distal uniserial portion. *G?* '*v. cf. venustus*' also appears similar to *Diplograptus bohemicus* (Marek, 1955) which Koren' *et al.* (1980) synonymize with their *G. persculptus* forma B. *D. bohemicus* is, however, used by Mu *et al.* (1974) as the top Ordovician zone fossil and I consider that this zone, which also contains *D. orientalis*, correlates with the top of the *P. pacificus* Subzone and the *C? extraordinarius* Zone at Dob's Linn (text-fig. 2).

G? '*v. cf. venustus*' appears to be restricted to the basal 0.46 m of Birkhill Shale at Dob's Linn;

although Legrand (1976) recorded '*C. venustus venustus*' to have a similarly restricted occurrence in the Sahara, he showed that '*C. v. venustus*' ranged longer. '*C. v. venustus*' has been reported recently from the 'basal Silurian' of Percé, Quebec (Léserpense and Sheehan 1981), and of the Gaspé Peninsula (Riva 1981). It therefore seems likely that the *G?* '*venustus*' species group may prove useful in correlating any future-defined Ordovician-Silurian boundary.

Genus AKIDOGRAPTUS Davies, 1929

Type species (by original designation). *Akidograptus ascensus* Davies, 1929, p. 9, text-figs. 22-24.

Revised diagnosis. ?*Climacograptus*-like thecae, first two protracted, growing upwards throughout most of their length.

Remarks. Bulman (1933, 1936) suggested that $th1^2$ might be lost, but in 1970 (p. VI31) stated that the proximal end was 'without definite uniseriate portion'. Stein (1965) concluded that development was complete. Rickards (1970) and Hutt (1974) retained *Akidograptus* in the Dimorphograptidae, but three-dimensional specimens from Dob's Linn indicate that proximal development is complete and the genus is therefore here assigned to the Diplograptidae as suggested by Stein (1965). Although *Akidograptus* had not been previously recorded earlier than the Silurian, Li and Ge (1981) recorded a new species *A. antiquus* from the late Ordovician *Tangyagraptus typicus* Zone of China.

Akidograptus ascensus Davies, 1929

Text-figs. 9f-h, 10j-n

- 1929 *Akidograptus ascensus* sp. nov. Davies, p. 9, text-figs. 22-24.
- 1933 *Akidograptus ascensus* Davies; Bulman, p. 16, pl. 3b, text-fig. 5.
- 1934 *Akidograptus ascensus* Davies; Hsü, p. 86, pl. 6, fig. 11a, b.
- 1936 *Akidograptus ascensus* Davies; Bulman, p. 25, text-fig. 2b.
- 1962 *Akidograptus ascensus* Davies; Tomczyk, p. 91, pl. 4, fig. 1; pl. 7, fig. 1.
- 1964 *Akidograptus ascensus* Davies; Yang, p. 634, pl. 1, figs. 6-11.
- ?1964 *Akidograptus giganteus* sp. nov. Yang, p. 635, pl. 1, fig. 13.
- 1965 *Diplograptus (Akidograptus) ascensus* Davies; Stein, p. 176, pls. 14f, 15b, text-figs. 22a, d, 23a-c.
- 1967 *Akidograptus ascensus* Davies; Obut *et al.*, p. 73, pl. 6, figs. 8, 9.
- 1971 *Akidograptus ascensus* Davies; Schauer, p. 53, pl. 11, figs. 4-6; pl. 12, figs. 6-10.
- ?1973 *Akidograptus cultus* sp. nov. Mikhaylova, p. 18, pl. 4, figs. 6, 7.
- 1974 *Akidograptus ascensus* Davies; Hutt, p. 55, text-fig. 9, figs. 9, 10.
- 1975 *Akidograptus ascensus* Davies; Bjerreskov, p. 42, text-fig. 13d, e.
- 1977 *Akidograptus ascensus* Davies; Rickards *et al.*, p. 98, text-fig. 7.
- ?1980 *Akidograptus ascensus cultus* Mikhaylova; Koren' *et al.*, p. 169, pl. 53, fig. 4; pl. 54, figs. 2-6; text-fig. 57a-c.
- 1981 *Akidograptus ascensus* Davies; Li and Ge, p. 227, pl. 1, figs. 1-2.

Holotype. SM A10021, the specimen figured by Davies (1929, text-fig. 23), from the Birkhill Shale, *P. acuminatus* Zone, Dob's Linn.

Material. The type material and about thirty specimens in my collections, mostly flattened but some in relief.

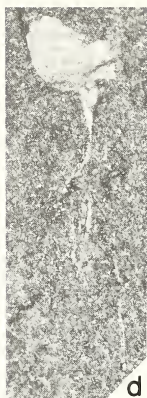
Horizons and localities. From 1.6 to 2.3 m above the base of the Birkhill Shale, low *P. acuminatus* Zone, Linn Branch trench, Dob's Linn.

Diagnosis. Small rhabdosome up to 1 mm wide with protracted $th1^1$ and 1^2 . Thecae, numbering about eleven in 10 mm, with almost vertical, straight supragenicular walls, rounded genicula, and short, straight, gently inclined intertheal septa. Apertures slightly everted, excavations narrow but long. Virgella commonly forked.

Description. The rhabdosome is up to 20 mm long with a protracted proximal region 0.2-0.3 mm wide and 2 mm long before the first thecal aperture. The width at the aperture of $th1^1$ is 0.3-0.5 mm, increasing rapidly to the maximum 0.8-1.0 mm in the following 2.5 mm, by the aperture of $th4^1$. The thecae number about eleven in



a



d



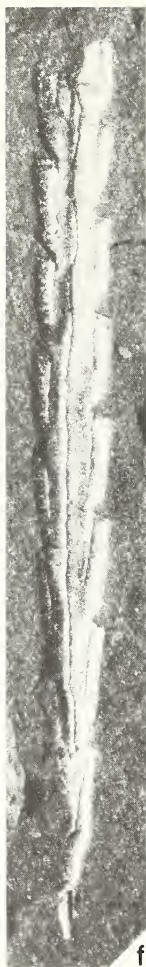
b



e



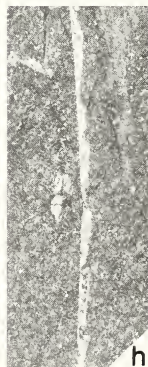
c



f



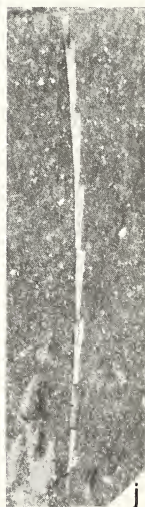
g



h



i



j

10 mm. The sicula is exposed for the whole of its 1.3 mm length and commonly possesses a bifurcating virgella. $Th1^1$ originates from towards the top of the metasicula and grows upwards for the majority of its length. After its presumed initial downward growth it runs sub-parallel to the sicula, then bends diagonally across the top. $Th1^2$ buds from $th1^1$ just below the apex of the sicula and grows straight upwards and slightly outwards. The remaining thecae are sub-alternate; they are long and thin and grow almost parallel to the rhabdosome axis but with a slight kink above the infragenicular wall. The supragenicular walls are straight and almost vertical with slight genicula. The apertures are slightly everted, opening into shallow excavations which occupy one-fifth the total width of the rhabdosome. The interthecal septa are straight and terminate above the level of the preceding aperture. A nema is normally present and commonly exceeds 5 mm long.

Remarks. The only British species which may be confused with *A. ascensus* are *Parakidograptus a. acuminatus* (Nicholson, 1867) and *P. acuminatus praematurus* (Davies, 1929). It is separable from both of these by its approximately *Climacograptus*-like thecal style, although the thecae of *A. ascensus* may appear similar to those of *P. acuminatus s.l.* when preserved in slightly oblique orientation. Davies recorded the proximal portion of *P. acuminatus praematurus* to be less protracted than either *P. a. acuminatus* or *A. ascensus*. *P. a. acuminatus s.s.* possesses more distinctly *Orthograptus*-like thecae which are straight with everted apertures. *A. giganteus* Yang, 1964 from the lower Silurian of China has *Climacograptus*-like thecae proximally, which become *Orthograptus*-like distally; this change may well be due to differential lateral spread on diagenetic flattening (Briggs and Williams 1981) and the species is doubtfully referred here to *A. ascensus*. *A. cultus* Mikhaylova, 1973 (*A. ascensus cultus* of Koren' *et al.* 1980) from the lower Silurian of the U.S.S.R. is very similar to *A. ascensus* but has thecae which sometimes have straight, inclined supragenicular walls, giving a somewhat *Orthograptus*-like appearance. Some specimens figured by Koren' *et al.* (1980) appear to be *A. ascensus s.s.* (e.g. text-fig. 57b, c) whilst others (e.g. text-fig. 57a) look like the forms considered here to represent *A. ascensus* that have suffered greater lateral spread at the apertures. Many similar specimens from the low *P. acuminatus* Zone at Dob's Linn do not conform strictly with the definitions of either *A. ascensus* or *P. a. acuminatus* and considerably more work needs to be done on these forms. Three new species, *A. antiquus*, *A. anhuiensis*, and *A. parallelus* were described by Li and Ge (1981), but translations of the descriptions are needed before any comment may be made concerning their distinctiveness.

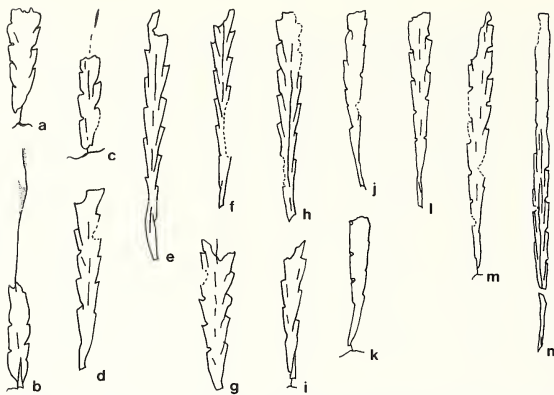
Both at Dob's Linn and the Lake District (Hutt 1974) *A. ascensus* is most typical of the lower part of the *P. acuminatus* Zone, where it is associated with *Atavograptus ceryx* (Rickards and Hutt 1970). *A. ascensus* appears to be widespread and is found outside Europe in China (Hsü 1934; Li and Ge 1981) and the U.S.S.R. (Obut and Sobolevskaya 1964). It is the most important species in determining the base of the *P. acuminatus* Zone.

Genus PARAKIDOGRAPTUS Li and Ge, 1981

Type species (by original designation). *Diplograptus acuminatus* Nicholson, 1867, p. 109, pl. 7, figs. 16, 16a.

Diagnosis (after Li and Ge). Rhabdosome with protracted proximal development. The sicula is almost completely free on the side of $th1^2$ and the lower half is free below $th1^1$, as in *Akidograptus*.

TEXT-FIG. 9. All from the Linn Branch trench, Dob's Linn. a-c, *Glyptograptus? avitus* Davies, 1929. *G. persculptus* Zone. a, HM C13886, juvenile with kinked nema, 1.46-1.56 m, $\times 10$. b, HM C13820/1, proximal end with branching virgella, 1.2-1.32 m, $\times 20$. c, HM C13892, nema with membranous growths, 1.56-1.66 m, $\times 10$. d, *Glyptograptus? avitus* Davies, 1929?, HM C13866, proximal fragment with branching virgella, 1.38-1.46 m, *G. persculptus* Zone, $\times 20$. e, juvenile *Climacograptus* sp. (cf. *C. normalis*) with membranous structures on virgella and nema, HM C13808, 1.1-1.2 m, *G. persculptus* Zone, $\times 10$. f-h, *Akidograptus ascensus* Davies, 1929, 2.01-2.14 m, *P. acuminatus* Zone. f, HM C14003, well-preserved specimen in partial relief, showing development of proximal end in reverse view, $\times 20$. g, HM C13998a, with kinked nema and showing proximal development although flattened, $\times 10$. h, HM C14002, proximal fragment preserved in relief, in reverse view, $\times 20$. i, j, *Atavograptus* sp., very narrow distal fragments, *P. acuminatus* Zone, $\times 20$. i, HM C13996b, 2.01-2.14 m. j, JM C14022, 2.19-2.31 m.



TEXT-FIG. 10. All from the Linn Branch trench, Dob's Linn, $\times 5$. *a-c*. *Glyptograptus? avitus* Davies, 1929. *G. persculptus* Zone. *a*, HM C13824/1, with somewhat thickened, forked virgella, 1.2–1.32 m. *b*, HM C13887, nema with membranous growths, 1.46–1.56 m. *c*, HM C13841, juvenile with slightly thickened nema and forked virgella, 1.2–1.32 m. *d-i*, *Parakidograptus acuminatus* (Nicholson, 1867) *sensu lato*, 1.66–1.79 m. *P. acuminatus* Zone. *d*, HM C13939. *e*, HM C13931. *f*, HM C13936. *g*, HM C13934/2, proximal fragment(?) with short first two thecae, similar to *P. acuminatus praematurus*. *h*, HM C13933/1. *i*, HM C13940, fragment showing proximal development and forked virgella. *j-n*, *Akidograptus ascensus* Davies, 1929, *P. acuminatus* Zone. *j*, HM C13925, 1.76–1.91 m. *k*, HM C13980a, showing forked virgella, 2.01–2.14 m. *l*, HM C13956a, in obverse view, showing proximal portion of sicula, 1.88–2.0 m. *m*, HM C13950, 1.88–2.0 m. *n*, HM C13982a, proximally in partial relief, 2.01–2.14 m.

Th1² is dicalycal, the median septum is complete. Thecae straight and inclined with simple, everted apertures.

Remarks. The erection of a new diplograptid genus with *P. a. acuminatus* as its type species is a reasonable solution to the problem of generic assignment of this species. Neither its position in *Akidograptus*, whose type species *A. ascensus* has a similar proximal development but different thecal style, nor questionably in *Orthograptus*, whose type species *O. q. quadrimucronatus* (Hall, 1865) has a more normal diplograptid proximal development and spinose thecae reinforced by apertural lists, was satisfactory. The many forms intermediate between *A. ascensus* and *P. a. acuminatus* s.s. found during this study (see *P. acuminatus* s.l. description) present a problem owing to distortion caused by both diagenetic and tectonic deformation. However, the erection *Parakidograptus* appears to solve more problems than it creates and it is therefore adopted here.

Parakidograptus acuminatus (Nicholson, 1867) *sensu lato*

Text-fig. 10*d-i*

?1867 *Diplograptus acuminatus* [sic] n. sp. Nicholson, p. 109, pl. 7, figs. 16, 16a.

?1908 *Cephalograptus? acuminatus* (Nicholson); Elles and Wood, pp. 289, 295, pl. 32, fig. 11a–d; text-fig. 199.

- ?1929 *Akidograptus acuminatus* mut. *praematurus* nov.; Davies, p. 10, text-fig. 25.
 ?1974 *Orthograptus? acuminatus acuminatus* (Nicholson); Hutt, p. 37, pl. 7, fig. 9; text-fig. 9, fig. 11; text-fig. 10, fig. 4.
 ?1974 *Orthograptus? acuminatus praematurus* (Davies); Hutt, p. 38, pl. 4, fig. 11.
 ?1981 *Parakidograptus acuminatus* (Nicholson); Li and Ge, p. 229, pl. 1, figs. 8-10.

Material. Many flattened fragmentary specimens in my collections.

Horizons and localities. From 1.6 to 2.3 m above the base of the Birkhill Shale, low *P. acuminatus* Zone, Linn Branch trench, Dob's Linn.

Remarks. The material assigned to *P. acuminatus s.l.* includes several specimens similar in size and overall form to *A. ascensus* but with rather elongate, *Orthograptus*-like thecae (text-fig. 10d-f). A few fragments, however, have an apparently less protracted proximal region and a greater maximum width up to 1.4 mm (text-fig. 10g). The former specimens have a similar distal thecal style to *P. acuminatus praematurus* but their proximal thecae are more protracted than those of the type specimens which Davies (1929) described from the *G. persculptus* Zone of the Lake District. The latter specimens have a more similar proximal development to this subspecies but have a more robust overall form and different thecal style. Rickards (1970) recorded both '*A.*' *a. acuminatus* and '*A.*' *a. acuminatus praematurus* to occur together in the '*A.*' *a. acuminatus* Zone of the Howgill Fells, northern England, but considered that the specimens of '*A.*' *a. acuminatus praematurus* may have represented a later survival. Toghil (1968b, p. 658) recorded '*A.*' *a. acuminatus* to be most common in the middle and upper parts of the '*A.*' *a. acuminatus* Zone at Dob's Linn.

Previous revisers of *P. a. acuminatus* have ignored the presumably mistaken spelling of the species name in the title of Nicholson's original description. As the spelling with one 'c' has been adopted by later workers and was apparently the version which Nicholson intended it is here adopted.

Li and Ge (1981) erected four new *Parakidograptus* taxa, viz. *P. acuminatus minimus*, *P. angustitubus*, *P. helixiensis*, and *P. huloensis*. Only one specimen of each is illustrated and until translations of the Chinese descriptions are available, comments on their affinities are not possible. *P. a. acuminatus* is a widespread species and has been recorded from the lower Silurian throughout the world.

Family MONOGRAPTIDAE Lapworth, 1873

Genus ATAVOGRAPTUS Rickards, 1974

Type species (by original designation). *Monograptus atavus* Jones, 1909, p. 531, text-fig. 18a-d.

Diagnosis (from Rickards 1974, p. 141). Long, slender, usually curved rhabdosome. Long sicula reaching to about the aperture of th1. Thecae generally elongatedly glyptograptid, but in some case strictly glyptograptid or almost monoclimacid.

Atavograptus ceryx (Rickards and Hutt, 1970)

Text-fig. 11a-f

- 1970 *Monograptus ceryx* sp. nov. Rickards and Hutt, p. 117, text-figs. 1a-d, 2a.
 1974 *Atavograptus ceryx* (Rickards and Hutt) Rickards, pl. 9, fig. 4.
 1975 *Atavograptus ceryx* (Rickards and Hutt); Hutt, p. 63, pl. 11, fig. 7.

Holotype. SM A67087, the specimen figured by Rickards and Hutt (1970, text-fig. 2a), from the Skelgill Beds, *G. persculptus* Zone, Yewdale Beck, Coniston, Lake District.

Material. Many specimens, preserved both flattened and in relief, in my collections. Most occur as crowded fragments on two bedding planes.

Diagnosis (after Rickards and Hutt 1970). Rhabdosome short with pronounced dorsal curvature, dorsoventral width 0.2 mm proximally to 0.3 mm distally. Sicula 1.5 mm long, apex reaching just above the level of the aperture of th1. Thecae with gentle sigmoidal curvature, horizontal to very slightly everted apertures, numbering thirteen to fifteen in 10 mm.



TEXT-FIG. 11. *Atavograptus ceryx* (Rickards and Hutt, 1970). 2.0–2.14 m, *P. acuminatus* Zone, Linn Branch trench, Dob's Linn. All $\times 20$ except *f*. *a*, HM C13993/1a. *b*, HM C14009/3a. *c*, HM C14010/1b. *d*, HM C14009/1a. *e*, HM C14010/2a. *f*, HM C14010/1-nb, general view of slab, $\times 2.5$.

Description. Most specimens are less than 5 mm long and possess a slight dorsal curvature. They increase slightly in width from an average 0.2 mm at the aperture of th1 to a maximum of 0.3 mm when not tectonically deformed. A thecal count is impractical because of the short stipes, but the distance between successive thecal apertures varies from 0.06 to 0.1 mm, depending on tectonic stretching and position along the stipe. This gives a thecal count of ten to sixteen in 10 mm. When undistorted the figure is nearer the thirteen to fifteen in 10 mm recorded by Rickards and Hutt (1970). The sicula is approximately 1.5 mm long (cf. 1.3–1.4 mm recorded by Rickards and

Hutt). Th1 appears to bud from near the base of the sicula and grow upwards parallel to it for its entire length. The thecae are variable in style depending on the orientation of the rhabdosome; three-dimensional specimens preserved in full dorsoventral orientation reveal them to be approximately *Glyptograptus* in style with gently curved supragenicular walls. The apertures are horizontal or slightly everted and open into long triangular excavations which occupy half the total stipe width. Slight genicula are seen when the stipes are preserved in dorsoventral orientation but the supragenicular walls appear straight and uniformly sloping when specimens are obliquely oriented. The interthecal septa are short and straight, extending for only half the length of the supragenicular walls.

Remarks. The specimens from Dob's Linn are similar to the type material of *A. ceryx* from the English Lake District and can definitely be assigned to this species. The thecal style appears similar to the distal thecae of *Akidograptus ascensus*, whilst Rickards and Hutt (1970) believed that *A. ceryx* could have been derived from a *Glyptograptus* ancestor. It is therefore possible that both *Akidograptus ascensus* and *Atavograptus ceryx* were derived from *Glyptograptus* ancestors. *A. ceryx* has a similar proximal development and thecal style to *Atavograptus atavus* (Jones, 1909) but has a higher thecal count (Hutt 1975, p. 63). Rare, unidentifiable fragments of a much narrower *Atavograptus* also occur in the *P. acuminatus* Zone at Dob's Linn (text-fig. 9i, j).

A. ceryx was first recorded by Rickards and Hutt (1970) from the *G. persculptus* Zone of the Lake District, but was later found by Hutt (1975) to occur also in the basal 0.6 m of the *P. acuminatus* Zone in the Skelgill Beds associated with *A. ascensus*; Hutt (1974) defined the base of the *P. acuminatus* Zone in the Lake District on the same criteria used in this work at Dob's Linn (i.e. principally on the first occurrence of *A. ascensus*) and I consider that the occurrence of *A. ceryx* in the low *P. acuminatus* Zone in both parts of Britain is contemporaneous. *A. ceryx* has not yet been recorded from outside Britain, although Rickards (1976a, p. 158) recorded that Sennikov (pers. comm.) had obtained a similar monograptid from the *P. acuminatus* Zone of the Altai Mountains, U.S.S.R.

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ORDOVICIAN GRAPTOLITES FROM THE GREAT PAXTON BOREHOLE, CAMBRIDGESHIRE

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ABSTRACT. The borehole penetrated beds with a lower Llanvirn fauna containing *Glyptograptus* cf. *denatus* (Brongniart), some other small and unidentified diplograptids, a *Paraulograptus*? sp., *Didymograptus pluto* sp. nov. (pendent), and a *Didymograptus* sp. (extensiform). The assemblage is quite different from others in Britain, but matches well with several from the Baltic and east European regions. *D. pluto* is described, with details of its proximal development, astogeny, and intrapopulation variation. Comparisons with *D. bifidus* (J. Hall) and *D. purchisoni* (Beck), which are species of quite different ages, show that convergent evolution strongly affected these pendent didymograptids. The different styles of proximal development (sicular shape, budding sequence) are the best means of unravelling these homeomorphies.

THE Llanvirn fauna of the Great Paxton borehole, 8 km south-west of Huntingdon in Cambridgeshire, England, is diverse and well preserved. It is of interest because it has the potential to provide clear evidence on the nature and development of the graptolites, trilobites, and brachiopods contained in the core. Additionally, as suggested in this paper and in Dewey *et al.* (1970), the sediments and the fauna were not related to deposits in the Welsh Basin or Skiddaw area of Britain, but were probably due to an extension of marine deposition eastwards from mainland Europe. Thus the fauna provides evidence bearing on the palaeogeography of the time.

Previous information on the fauna has been published by Stubblefield (1967) and Skevington (1973). In the former, only preliminary identifications of the graptolites and trilobites were listed. The more detailed account in Skevington (1973) attempted description of the fauna in terms of the existing taxonomy for pendent didymograptids. Unfortunately, that taxonomy was strictly typological, so that too-narrowly defined 'species' were distinguished within what is now known to be the intraspecific variation of a single pendent didymograptid species. The same study did not cover the highly important aspect of proximal development in the pendent species, and did not identify all the graptolite species in the core. The present paper gives attention to these problems and provides a full reassessment of the age and importance of the fauna.

STRATIGRAPHY, AGE, AND PROVINCIAL RELATIONSHIPS

Stubblefield (1967) and Skevington (1973) have provided most of the necessary details of the location, stratigraphy, and palaeogeographical importance of the borehole. The Llanvirn shales young upwards through the core and are overlain unconformably by Liassic (Jurassic) strata. The top 0.5 m or so of Ordovician beds are bleached and deeply weathered; when unweathered they are grey, uncleaved shales and mudstones interbedded with pale micaceous sandstones and siltstones. The graptolite rhabdosomes are sometimes current-oriented parallel to the strike (150°; Skevington 1973). The core was discontinued after penetrating 27.7 m stratigraphic thickness of Llanvirn beds.

Skevington (1973) assigned the fauna to the upper Llanvirn *D. purchisoni* Zone, based largely on the identification of individuals in the fauna that could be matched in their stipe and thecal dimensions to the type specimens of *D. purchisoni* (Beck), *D. purchisoni* cf. *geminus* (Hisinger), *D. purchisoni speciosus* Ekström, *Glyptograptus* cf. *euglyphus* (Lapworth), and *Climacograptus pauperatus* Bulman. However, reidentification of all the material indicates that none of these forms is in fact present. Instead, the evidence now supports an early Llanvirn age assignment.

The several pendent didymograptid varieties identified by Skevington (1973) are now known to

belong to a single morphologically variable species—*D. pluto* sp. nov.—which is abundant throughout the core. Although outwardly this species shows a very close resemblance to the upper Llanvirn species *D. murchisoni* in the size and shape of its rhabdosome, it is quite different, particularly in its mode of proximal development. In this aspect, its most exact comparison is to the form described as '*Didymograptus* n. sp. b. aff. *D. minutus* Törnquist 1879' in Skevington (1965) from the very lowest beds of the lower Llanvirn '*D. bifidus* Zone' of Öland (Sweden). It is also similar in many of its dimensions to *D. pakrianus* Jaanusson (1960) from Pakri in Estonia, though there are some differences, and the proximal thecal development of *D. pakrianus* remains undescribed. *D. pluto* does not resemble any of the pendent species described from the Ordovician of Britain.

Further indications of an early Llanvirn age are derived from comparisons of the other species with some graptolite occurrences in the Baltic region and in Czechoslovakia. *Glyptograptus dentatus* is widespread in the lower Llanvirn (Bulman 1963; Skevington 1965, 1970) and the occurrence in the borehole of closely related material is suggestive of this level. Jaanusson (1960) recorded a form '*Didymograptus?* sp. C.' from the same beds as *D. pakrianus* at Pakri in Estonia, which is very nearly identical to the *Paraulograptus?* sp. now identified in the borehole. Although the graptolite fauna of the Pakri Beds has not in itself yielded a conclusive indication of age, the unit in which it occurs is regarded as early Llanvirn (Jaanusson 1960, p. 344, table 9). The genus *Paraulograptus* was first described from the lower Llanvirn *Corymbograptus retroflexus* Zone of Czechoslovakia (Bouček 1973). An extensiform didymograptid species closely comparable to such Arenig species as *D. formosus* Bulman (1936; Archer and Fortey 1974) also occurs in the borehole and lends further support to an early rather than late Llanvirn age. The unidentifiable diplograptids provide no further accurate age information.

From the above comments on correlation, it is clear that the fauna has strong provincial relationships with the Llanvirn faunas of the Baltic and east European regions. On the other hand, it is markedly different from the typical lower Llanvirn assemblages of Wales, Shropshire, and northern England. For instance, *D. artus* Elles and Wood, *D. nicholsoni*, and *G. dentatus* dominate those faunas but are absent or rare in the Great Paxton Borehole, where instead *D. pluto* and *Paraulograptus* sp. are dominant. Neither of these has previously been recorded in Britain.

Thus the evidence suggests that the Cambridgeshire area in the Llanvirn was dominated by marine influences from mainland Europe, but was rather isolated from the faunas of Wales and neighbouring areas. Whether this was due to blocking by emergent areas or to large-scale facies control (? with the *D. pluto* fauna as a shallow water facies) is at present unknown.

SYSTEMATIC PALAEOLOGY

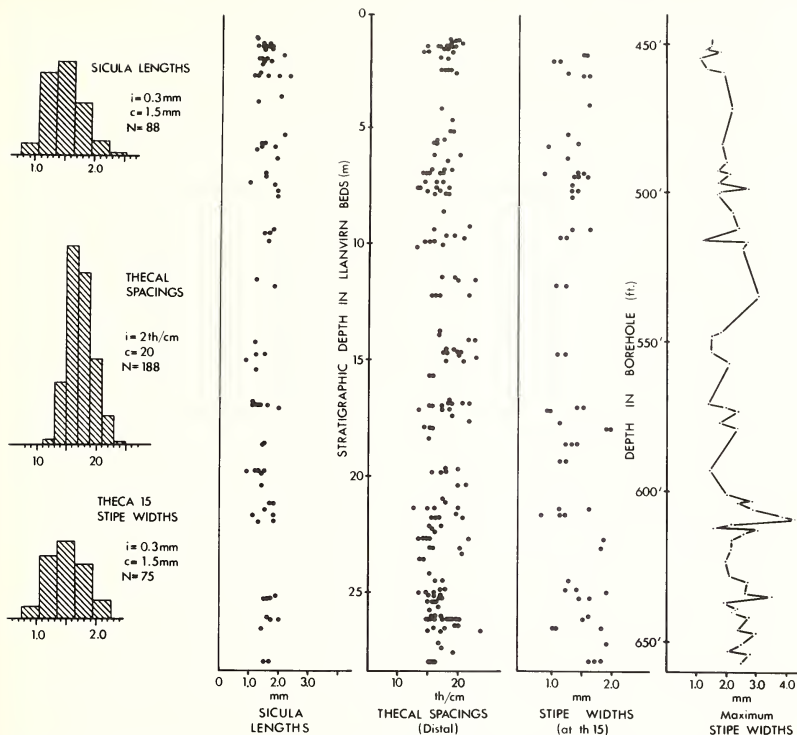
The morphological terms employed here are those of Bulman (1970). Several additional points need to be noted in connection with the biometric statistics. Measurements of sicula length were not taken from specimens with proximal cortical overgrowths. Proximal stipe divergence values were measured on dorsal margins of the stipes, directly adjacent to the sides of the siculae. Stipe widths were measured at 5-theca and not 5 mm intervals down the stipes, as has been more usual in past descriptions. This has been to ensure strictly homologous comparisons between those individuals and species with different thecal spacings. The characters 'distal stipe width' and 'stipe length' were measured on the full range of astogenetic growth stages and do not represent maximum values applicable only to the most mature stages of growth. Standard statistical parameters are abbreviated as: Mean ($\bar{X}$), Sample size (N), Maximum (max.), Minimum (min.), and Standard Deviation (σ). The Variation Coefficient (V_c) gives a dimensionless guide to the variability of a character and is the ratio $S/\bar{X}$. A rather more informal statistic reflecting the observed ranges of variation and which is employed in comparisons in a later section is termed the 'Range coefficient' (R_c). It is equivalent to whichever is the larger of $(X_{\max} - \bar{X})/\bar{X}$ and $(\bar{X} - X_{\min})/\bar{X}$.

Family DICHOGRAPTIDAE Lapworth, 1873

Genus DIDYMOGRAPTUS M'Coy, 1851

Didymograptus pluto sp. nov.

Text-figs. 2A, B, 3A–U, 4A–C



TEXT-FIG. 1. Biometric characters of *Didymograptus phuto* sp. nov. through the Great Paxton Borehole core. Depths down the borehole are recorded in feet below the surface (as originally logged), but a supplementary scale is also given to show the true (dip corrected) thicknesses in metres below the base of the overlying Jurassic. For the histograms N = number of measurements, i = class interval, c = centre point of one of the classes.

- cf. 1965 '*Didymograptus* n. sp. b. aff. *D. minutus* Törnquist, 1879' Skevington, p. 22, figs. 27–29.
 1973 *Didymograptus acutus* Ekström, 1937; Skevington, p. 44, text-fig. 1a–c.
 1973 *D. cf. acutus*; Skevington, p. 45, pl. 8, fig. 2; text-fig. 1d–g.
 1973 *Didymograptus artus* Elles and Wood, 1901; Skevington, p. 46, text-fig. 2a–f.
 1973 *D. cf. artus*; Skevington, p. 47, pl. 8, fig. 1; text-fig. 2g–j.
 1973 *Didymograptus munchisoni* (Beck) 1839; Skevington, p. 47, pl. 8, figs. 3–5; text-fig. 3a.
 1973 *D. munchisoni speciosus* Ekström, 1937; Skevington, p. 48, pl. 9, figs. 1–5; text-fig. 3b.
 1973 *D. munchisoni cf. geminus* (Hisinger) 1840; Skevington, p. 49, pl. 8, fig. 6; text-fig. 3c.

Holotype. By8204 (text-fig. 3g herein and pl. 8, fig. 2 of Skevington 1973), from the 410 ft level of the borehole.

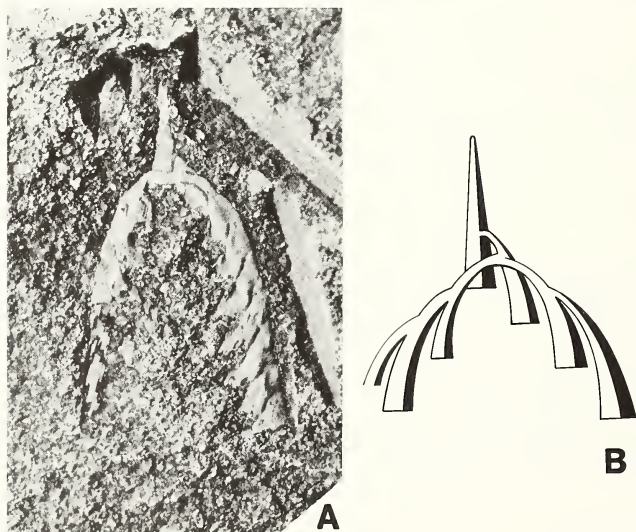
Material. Over 220 specimens (within the bracket of numbers By8110–9209; Institute of Geological Sciences, London); they included those described and figured by Skevington (1973).

Diagnosis. Pendent didymograptid with a dicalyca $th1^2$ and with $th1^1$ originating low down on a sicula which averages 1.5 mm in length. Stipes reach 3–4 cm in length and 2.0–4.3 mm in width at $th30$ and beyond. Average stipe width at $th10$ is 1.25 mm. Average spacing of distal thecae is 17 th/cm (range 13–23 th/cm).

Derivation of name. After the mythical ancient Greek god of the underworld.

Description. The siculae range between 2.3 and 0.9 mm in length and are 0.3–0.4 mm wide at their apertures when flattened. They are straight-sided and conical in form and are positioned axially in the rhabdosomes without any significant leaning to one stipe or the other. $th1^1$ buds from c. 0.4–0.5 mm above the sicular aperture and grows down, confluent with, but slightly oblique to the sicula before diverging abruptly at an angle of 45° . It grows to about 0.4–0.5 mm in width (flattened) over its total length of 0.7 mm. $th1^2$ buds from the reverse and sicular side of $th1^1$ at a level about 0.3 mm below the $th1^1$ origin on the sicula. $th2^1$ appears on $th1^2$ almost immediately afterwards, so that the development is clearly *D. minutus* Stage in the sense of Bulman (1970) (text-fig. 2). The crossing canal portion of $th1^2$ is about 0.13 mm wide and runs horizontally across the sicula for about 0.3 mm before turning downwards to form stipe 2. $th2^1$ is a similar width as it crosses $th1^1$ to initiate stipe 1. The level of the aperture of $th1^2$ lies midway between that of $th1^1$ and $th2^1$.

The stipe widths average approximately 0.7 mm at $th1$, 1.0 mm at $th5$, 1.25 mm at $th10$, 1.5 mm at $th15$, and 1.9 mm at $th25$ but typically vary within a range of $\pm 40\%$ of these means (Table 1). The usual maximum stipe widths of 2.0–3.0 mm (but up to 4.3 mm) are attained by $th30$. The thecae are spaced at an average of 17 th/cm distally (range 13–23 th/cm) but in most cases are slightly more closely spaced proximally. $th1$ has a 0.43 mm long free ventral wall, but in the distal thecae this may reach 0.7 mm. The intertheical septa are generally 2.0 mm long, 0.5 mm apart (when flattened), and are usually inclined at 30 – 50° to the dorsal margins of the stipes. Growth in the length of each individual theca apparently continued throughout astogeny, particularly on the proximal thecae, so that stipe widths of 1.0 mm are often recorded at $th1$ – 2 on mature individuals even though in the early



TEXT-FIG. 2. *Didymograptus phuto* sp. nov. A, specimen By9055, preserved in partial relief, showing proximal development, $\times 12$. B, diagram of development.

stages this width is only 0.5–0.7 mm. The more mature individuals may also bear a proximal cortical membrane overgrowth over the siculae and early thecae (text-figs. 3*a–d*).

The stipe divergences are usually 80–110° proximally but tend to become sub-parallel distally (range: –10° to 70°).

Discussion. Table 1 and text-fig. 1 show that the entire collection of pendent didymograptids from the borehole represents successive populations of one slowly evolving species. The frequency distributions for the biometric characters are all unimodal. The amount of change in these characters through the core is negligible for almost all characters.

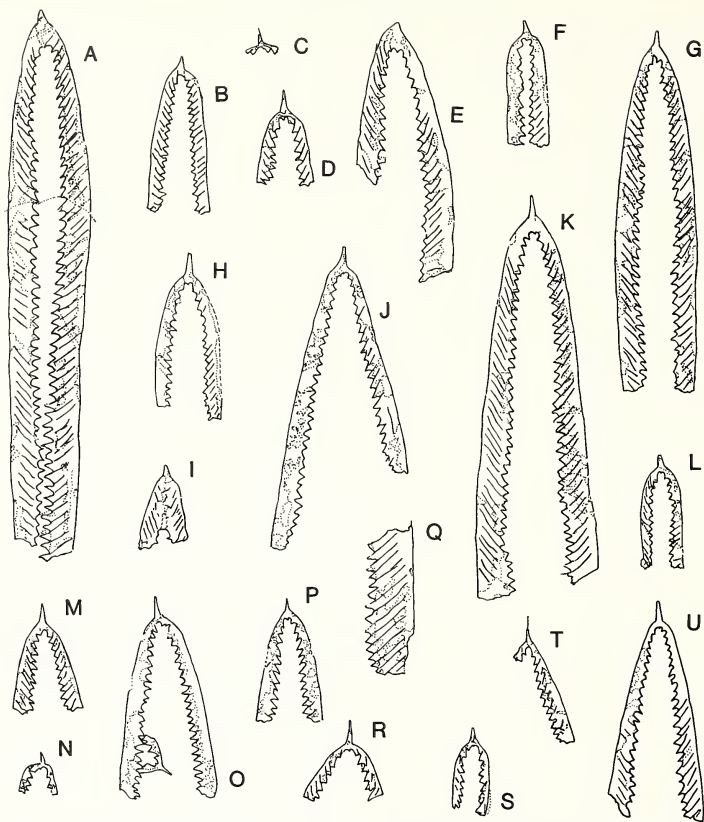
TABLE 1. Biometric statistics of *Didymograptus pluto*. All measurements in millimetres unless otherwise indicated.

Statistics:	<i>N</i>	$\bar{X}$	<i>S</i>	<i>V_c</i> (%)	max.	min.	<i>R_c</i> (%)
Characters:							
Sicula lengths	87	1.51	0.28	19	2.3	0.93	52
Theca 1 stipe widths	187	0.66	0.17	25	1.12	0.4	70
" 5 " "	178	1.01	0.19	19	1.84	0.6	82
" 10 " "	132	1.26	0.22	17	1.8	0.8	42
" 15 " "	74	1.49	0.28	19	2.05	0.9	39
" 20 " "	40	1.66	0.33	20	2.2	1.2	32
" 25 " "	13	1.79	0.18	10	2.4	1.5	34
Distal stipe widths	271	1.50	0.64	43	4.3	0.45	187
Proximal thecae/cm	154	18.6	2.04	11	23.8	12.8	31
Distal thecae/cm	188	17.2	2.2	13	22.7	13.2	32
Proximal stipe divergences	68	92.4°	22.5°	24	200°	35°	116
Distal stipe divergences	67	17.3°	28.6°	24	160°	–8°	825
Stipe lengths	132	12.3	9.8	80	43.0	3.0	250
Distal thecal inclinations	107	43.3°	8.5°	20	65°	10°	77

The exceptions are the distal and th15 stipe widths, which both decrease upwards through the core. Two samples of ten specimens each show a difference in average distal widths of between 2.5 mm at the bottom of the core, and 1.6 mm at the top. The effect is certainly statistically significant, but it correlates with no other changes of morphology and is not regarded as important above the subspecies level. The fact that the size decreases upwards in *D. pluto* is important because it is in contrast to the usual observation of size increases in pendent didymograptid evolution. Unfortunately, it is not known whether the size decreases were directly the result of environmental changes upwards through the core, or whether they involved real (genetic-based) evolution within the species.

The pendent didymograptid taxa that were recognized in the same collection by Skevington (1965) were therefore morphotypes (see George 1971)—narrow, typologically defined, and conspecific varieties. Summed together they represent the normal range of intraspecific (genetic, astogenetic, environmental, and preservational) variations. Thus, the '*D. artus*' variety recognized by Skevington embraced the small (i.e. young) astogenetic growth stages of *D. pluto* that have high values of thecae/cm, while the form '*D. acutus*' represented the same, but with lower numbers of thecae/cm. The varieties '*D. munchisoni munchisoni*' and '*D. munchisoni speciosus*' referred to a similar variation in thecal spacings amongst the mature growth stages. Individuals in which the stipes widened very noticeably were assigned to '*D. munchisoni cf. geminus*'. All these and their accompanying 'cf.' varieties are now placed within the morphological range of *D. pluto*.

The proximal development of the species is shown clearly in two pyritized specimens (e.g. text-fig. 2) and in a few specimens at the top of the core, which were made semi-transparent by weathering prior to the Jurassic. It is comparable in nearly every way to the development of the '*Didymograptus*



TEXT-FIG. 3. *Didymograptus pluto* sp. nov., Great Paxton Borehole; representative sample of specimens showing the full width of the intraspecific variation, all $\times 3.0$. A, By8669; B, By9130; C, By8117; D, By9055; E, By8921; F, By8291; G, By8204; H, By8267; I, By8985; J, By8327; K, By9093; L, By8549; M, By8127; N, By8231; O, By8911; P, By8144; Q, By8911; R, By8224; S, By8211; T, By8198; U, By8205.

n. sp. b. aff. *D. minutus* Törnquist 1879' of Skevington (1965) and its synonym, the '*D. minutus* MUT. Holm' of Bulman (1936, 1970), which together should now be regarded as representing a small-sized subspecies of *D. pluto*. The similarities of basic developmental features and of dimensional aspects (like sicula length, crossing canal widths, thecal lengths, etc.) at the proximal ends means that at their early growth stages they are virtually indistinguishable.

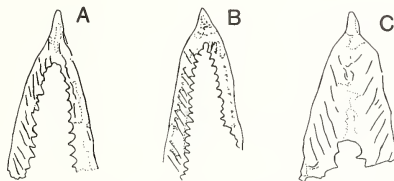
D. pluto is not closely related to the original *D. minutus* Törnquist from the Upper Arenig of Sweden. Skoglund (p. 25 in Skevington 1965) reported that the true *D. minutus* has a dicalycal th1¹ and

Skevington (1965) noted that its sicula is different from that in his '*D. n. sp. b. aff. minutus* Törnquist 1879', which as noted above is identical to *D. pluto* at its proximal end.

D. pluto may be closely related to the following species:

(a) *D. pakrianus* Jaanusson, 1960 (lower Llanvirn of Estonia). This is very similar in its general dimensions and overall morphology (e.g. in the presence of proximal cortical overgrowths at maturity). The thecal spacings, however, range somewhat lower than in *D. pluto* (15.0–17.5 th/cm), and the rhabdosomes have a smaller size at full maturity. Unfortunately the proximal development of the species is unknown.

(b) *D. paraindentus* Berry, 1960 (upper Arenig, Texas) resembles many of the younger growth stages of *D. pluto*, most markedly in overall shape and size, and in the shape and disposition of the sicula. The only described specimens of *D. paraindentus* are flattened and the proximal development is unknown.



TEXT-FIG. 4. Proximal ends of mature growth stages of *Didymograptus pluto* sp. nov., illustrating the cortical overgrowths and thecal enlargement relative to young growth stages. A, By8922; B, By9181; C, By8985; $\times 4$.

Although certain specimens of *D. pluto* may be compared with collections of the following species on the basis of resemblances in a selection of characters, they are really quite different.

(a) *D. murchisoni* is similar in sicular size and rhabdosomal shape and size, and both develop proximal cortical overgrowths at maturity. *D. murchisoni*, however, has a wider thecal spacing (average 14.3 th/cm for topotypes) and th^1 is dicalycal (text-fig. 6B).

(b) *D. artus* Elles and Wood, 1901 also develops proximal overgrowths and has broadly similar thecal spacings (15–16 th/cm) but rarely reaches such great sizes as *D. pluto*. Like *D. murchisoni* it has a dicalycal th^1 (unpublished work by the author).

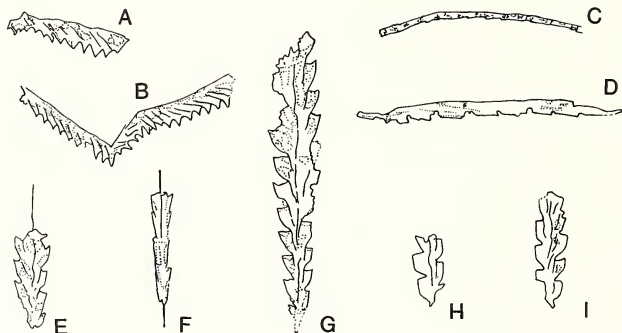
(c) *D. bifidus* (Hall)—as shown by collections from the type area of Quebec, Canada (e.g. SM A17307–8 Sedgwick Museum, Cambridge)—has similar stipe width and thecal spacing values to *D. pluto* and has a dicalycal th^1 . It differs in the rather short and squat shape of the sicula, and the high (probably prosicular) origin of th^1 from the sicula. Stipe divergences are significantly higher, especially proximally.

NOTES ON THE REMAINDER OF THE FAUNA

The extensiform didymograptid is a new discovery in the core. The material comprises just one proximal end and a distal stipe fragment (483 and 469 ft levels). It has a 1.3 mm long sicula with little supradorsal projection. In this it greatly resembles *D. cypselo* Archer and Fortey (1974). The thecae are spaced at 13.3 th/cm proximally but at 11 th/cm on the distal fragment, where the stipe width reaches 1.4 mm. The stipes are declined proximally and enclose about 160°. The material is too

limited for positive identification but a certain overall similarity to the form '*Expansograptus huddlicensis*' Bouček (1973) should be noted.

Little can be added to the description in Skevington (1973, text-figs. 3d-f) of the unusual fragile-stiped aulograptid that was labelled then as '*Didymograptus?* sp.' and '*Aulograptus?* sp.' These varieties represent preservational modes of the one species. The stipes are long, very thin, and apparently extensiform, though in the absence of specimens with a proximal end this is difficult to verify. The species is obviously closely related to the '*Didymograptus?* sp. C.' of Jaanusson (1960), as Skevington (1973) recognized. Bouček (1973) more recently described another similar form from Czechoslovakia as *Paraaulograptus*. The type species, *P. expectatus* Bouček, has thin, fragile extensiform stipes with aulograptid thecae and obviously represents the same type of graptolite as the Great Paxton borehole species, which, accordingly, is now identified as '*Paraaulograptus?* sp.' Imperfect material of *Paraaulograptus* like this is distinguished from collections of *Aulograptus* by being thinner and by the length of the stipes. The more robust stipes of *Aulograptus* appear to have been less susceptible to fragmentation and collections always contain a large proportion of intact pendent rhabdosomes.



TEXT-FIG. 5. A, B, *Didymograptus* sp. (extensiform); A, By8282; B, By8237. C, D, *Paraaulograptus?* sp.; C, By8174; D, By8567. E-F, H-I, diplograptids (unidentified); E, By8126; F, By8657; H, I, By9001. G, *Glyptograptus* cf. *dentatus* (Brongniart), By8122. All $\times 8$ except A, which is $\times 4$.

Diplograptids occur sparsely through almost the entire length of the core at levels between 449 and 651 ft. However, few are identifiable. Most are fragmentary, preserved in subscleriform views, or are at too young a growth stage for effective identification (text-fig. 5f, h, i). One large specimen, though, is identified as *Glyptograptus* cf. *dentatus*. Its salient characters are: maximum length 9 mm; thecal spacings c. 10 th/cm proximally and 15 th/cm distally; maximum stipe width 1.6 mm (flattened). The proximal ends are strongly tapered and only 0.7 mm wide at th1. The sole ornamentation is a short virgella; the median septum is gently and sinuously curved. The thecae have quite convex profiles and wide apertural excavations. The interthecal septa are only short and simple and originate at a level above the previous thecal aperture. The differences between this form and *G. dentatus* proper include its closer thecal spacings, lack of apertural spines on th1, and smaller overall size (though this may be an artefact of the small number of specimens available or of the local environment at the time of deposition). The form may be closely related to the *G. dentatus* recorded from Öland (Sweden) by Skevington (1965).

DISCUSSION

Intrapopulation variation. Case studies of the intrapopulation variation in graptolite species have been rare. The Great Paxton borehole collection provides an excellent opportunity to illustrate this important phenomenon in a dichograptid graptolite.

The collection contains over 200 well-preserved individuals of *D. pluto* representing all stages of astogenetic growth. It has been pooled from a number of small collections of up to eleven specimens per 30 cm length of core. This pooling will have certain effects on the statistics and their interpretation. For instance, because of the changes in some values through the 25 m stratigraphical range, the variations shown in Table 1 are really intraspecific (rather than intrapopulation). This is not an important distinction for most characters (i.e. all except for the distal stipe width) because for most characters the upwards changes were negligible and the scatter of values in any one population is roughly equivalent to the scatter observed in the whole sample. Pooling will have the fortunate effect of smoothing out short-term (i.e. seasonal) variations in the species.

Table 1 sets out the primary biometric statistics for the collection. It shows that intrapopulation variations of the order of ± 0.5 mm in the sicula lengths, of $\pm 4-5$ th/cm in the thecal spacings, of up to 140° in distal stipe divergences, and of up to 4 cm in stipe lengths occur, and should perhaps be expected more generally in didymograptid species.

The variations can also be expressed in terms of Variation Coefficients—useful parameters for comparing between species and characters (Simpson *et al.* 1960). For most characters they lie in the range 10–30% (e.g. for thecal spacings, sicula lengths, and stipe widths beyond th5). In such cases the low variability is usually confirmed by the small total ranges, and the 'Range coefficients' are seen to measure about 25–40% of the mean values. Characters with this low type of variability will be the most useful in species diagnosis. Basic features of the proximal development have a very low variability (are virtually constant) and will also be highly useful.

In contrast, characters like th1, th5, and maximum stipe widths, the stipe divergences and stipe lengths have very large amounts of variation indeed ($V_c \geq 20-80\%$, $R_c \geq 30-200\%$). They must be of little value in discriminating between species.

Intrapopulation variations in graptolites stem from a variety of causes which act unequally on the characters. Included amongst the causes are natural genetic variations within the gene pool, astogenetic growth, environmental (ecophenotypic) effects imposed during life, and preservational vagaries. The intrapopulation variations shown by *D. pluto* (Table 1) are an illustration. The characters with the smallest degrees of variation, such as the thecal spacings, sicula lengths, and stipe widths beyond th5, probably had their variations determined largely by genetic processes. Because rhabdosomes cannot undergo changes in length during diagenetic compression, thecal spacings and sicula lengths are immune from preservational variations, except perhaps for breakages prior to burial.

Most other characters have strong superimposed preservational variations. The very great change in overall size from the sicula stage up to the th5 stage in *D. pluto* accounts for the observed wide variations in stipe lengths and maximum stipe widths. Cortical thickening and continued growth of the thecae at the proximal end during astogeny probably accounts for the relatively high variabilities observed in the th1 and th5 stipe widths. A preservational phenomenon that will strongly affect the stipe widths beyond th5 and the thecal inclinations is the flattening of the stipes when they are caught in a variety of orientations from profile to scalariform during burial. This will induce wide variations in stipe widths and thecal inclinations. Finally, the chance factors involved when rhabdosomes settle into the sediment will strongly affect the measurements of the distal stipe divergences.

Morphotypes. Similar variations to those found in *D. pluto* are predicted to occur in the majority of species-collections of pendent didymograptids and other dichograptids. Thus, it is of no use describing collections of these graptolites in terms of morphotypes with very constricted ranges of variation (fractions of the real intrapopulation variation). Such taxa—like those in Skevington (1973)—will have no natural genetic or phylogenetic significance.

It is instructive to look at the narrowness of the variation that has been allowed in morphotypes, in comparison to actual intrapopulation variations. This can now be done in the case of the morphotypes of Skevington (1973), which are covered by the ranges of variation in *D. pluto*. Obviously the morphotypes constitute narrow and artificial divisions of the real species.

	Skevington morphotypes	<i>D. pluto</i> collection
Thecae/cm	± 2–3	± 4.0–5.8
Stipe widths	± 0.3–0.5 mm	± 0.7–1.2 mm
Max. stipe widths	c. 1.5 mm	c. 4.0 mm
Distal stipe divergences	± 20–30°	–25°–+140°
Stipe lengths	c. 12 mm	c. 40 mm

Unfortunately the use of narrow morphotypes is traditional in pendent didymograptid systematics. Many well-known taxa in Elles and Wood (1901–18), Bulman (1931), Ekström (1937), Decker (1944), Ruedemann (1947), Lemon and Cranswick (1956), Berry (1964, 1970), and Bouček (1973) are morphotypes that have been identified only by comparisons with one or a few type specimens. While the taxa of these papers may be familiar, in fact the characteristics of their populations are almost completely unknown. A conversion to population-defined units will be required before much progress can be expected in understanding the stratigraphical record of the pendent didymograptids.

Evolution and biostratigraphy. It is a widely held belief that the pendent didymograptid group was highly conservative in its evolution (Bulman 1958, p. 116; Bergström and Cooper 1973, p. 335). This view is incorrect. The faunas at separate levels do appear superficially the same in terms of stipe dimensions and thecal spacings, but this was probably due to convergent evolution producing repeated homeomorphs in stipe and thecal dimensions. In contrast, styles of proximal thecal development appear to be characteristic of separate groups of species which have restricted stratigraphical ranges (see below). This feature, and the complexity of the patterns of proximal development (which makes it unlikely that they were affected by convergent evolution), both suggest that the proximal end structure of these graptolites can be used very effectively in outlining the true lines of descent in the group.

Here the principle is used to illustrate the convergences that affected *D. pluto*, *D. munchisoni*, and also *D. bifidus*.

First, it is observed that the three species have very different modes of proximal development. Given the importance of this character for taxonomy within the group, this suggests that all three were not closely related—in spite of their similarities (convergences) in thecal and stipe dimensions.

The developmental characters (see text-figs. 2 and 6) are as follows:

(a) *D. bifidus* has a high point of origin (? from prosicula) for $th1^1$ from the sicula, $th1^2$ is dicalycal, and the sicula is usually short, inflated, and paired to some extent with the $th1^1$.

(b) *D. pluto* has a low origin for $th1^1$ from a long, straight-sided, and isolated (unpaired) sicula; $th1^2$ is dicalycal.

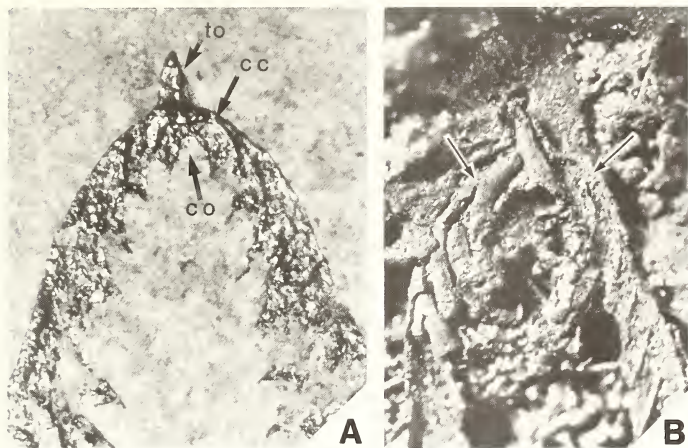
(c) *D. munchisoni* has a low origin for $th1^1$ from a long and isolated (unpaired) sicula, and $th1^1$ is dicalycal.

Work in progress by the author indicates that each species represents one of three major subdivisions of the pendent didymograptid group. The subdivisions may have been related or derived independently from other dichograptids, but in any case they have a clear pattern of stratigraphic occurrence:

Group (a) lower to upper Arenig; the *D. bifidus* from Quebec is lower Arenig and occurs with *Tetraraptus fruticosus* (Hall).

Group (b) ?upper Arenig to lower Llanvirn; *D. pluto* is lower Llanvirn.

Group (c) upper Arenig to upper Llanvirn; *D. munchisoni* is upper Llanvirn.



TEXT-FIG. 6. A, *Didymograptus bifidus* (J. Hall), lower Arenig, 'Point Levis, Quebec', Canada; SM A13703-8, preserved in partial relief, showing proximal development; note crossing canal (CC) leading to $th2^1$ passing reverse side of $th1^1$, and slight cortical overgrowth (CO) between the sicula and $th1^1$; $th1^1$ originates at the level marked 'TO'. B, *Didymograptus munchisoni* (Beck), upper Llanvirn, Abereiddi Bay, Dyfed, Wales; SM A24630, preserved undeformed and in full relief inside a pyrite nodule; arrows point to origins of $th1^2$, and $th2^1$ (note traces of intertheatal septa). Both $\times 12$.

These ranges support the arguments which maintain modes of proximal development as the prime means of separating lines of descent in the pendent didymograptid group. Thecal, stipe, and general rhabdosomal dimensions are of no use for this purpose as they suffered repeated instances of evolutionary convergence. This, and a reliance on such dimensions in the identification of species, are what have made the biostratigraphy of the group so difficult.

The extent of convergence in rhabdosomal form that can be shown by unrelated species of different ages is illustrated in Table 2. This shows that for *D. bifidus*, *D. pluto*, and *D. munchisoni*, ranges of intrapopulation variation in stipe width, stipe length, stipe divergence, thecal spacing, and even sicula length overlap enormously. This is a clear case of homeomorphy (convergence) between unrelated and age-separated species.

The result of this overlap is that rhabdosomes looking very much like typical *D. munchisoni* are found commonly in collections of *D. pluto* (cf. pl. 3, figs. 1-3 in Elles and Wood (1901-18) with text-figs. 3A, G, K herein). It was precisely this convergence in general form which permitted Skevington (1973) to misidentify some individuals of *D. pluto* with *D. munchisoni*—in spite of the great differences at the proximal ends.

The convergences between *D. pluto* and *D. bifidus* are at the stage of the younger rhabdosomes and are concerned more with thecal spacings. Thus, a morphotype which has been confused and identified in collections of both species is '*D. artus*' (e.g. Skevington 1973; Berry 1970). The real *D. artus* is a lower Llanvirn species and is different from *D. bifidus* and *D. pluto* in—amongst other things—its proximal development. Reports of a very long stratigraphical duration (Arenig-Llanvirn) for *D. artus* are wrong and are based on the identification of homeomorphs similar in their

TABLE 2. Comparison of the biometric characters of *Didymograptus bifidus*, *D. pluto*, and *D. munchisoni*. All measurements are in millimetres unless otherwise stated. Details of collections of *D. bifidus* and *D. munchisoni* are from unpublished work by the author.

	Species:	<i>D. bifidus</i> (Hall)	<i>D. pluto</i> sp. nov.	<i>D. munchisoni</i> (Beck)
	Horizon:	Lower Arenig	Lower Llanvirn	Upper Llanvirn
	Material:	SM A13707-8	By8110-9209	GSM 6820 b
Number of specimens		8	220	35
Sicula lengths		1.3-1.7	0.93-2.3	1.4-1.7
Theca 10 stipe widths		1.9-2.5	0.8-1.8	1.3-2.0
Distal stipe widths		2.1-3.7	1.5-4.3	2.0-3.4
Distal thecae/cm		14.3-16.6	12.8-23.8	12.5-16.7
Proximal stipe divergences		99°-122°	35°-116°	72°-119°
Distal stipe divergences		39°-50°	-8°-160°	-10°-13°
Maximum stipe length		30	43	4
Localities		'Point Levis, Quebec, Canada.'	Great Paxton Borehole, Cambridgeshire. (Topotypes)	Gelli Hill, Builth Wells, Wales. (Type-slab)

stipe and thecal dimensions to the holotype specimen of '*D. artus*' in a range of faunas at different levels.

CONCLUSIONS

Phylogenetic and biostratigraphical studies of pendent didymograptid faunas are likely to fail or err badly unless (1) diagnostic characters of the species are determined with reference to their intraspecific variation, and (2) attention is given to the styles of proximal development. In cases where this is not practised, confusion will develop between unrelated homeomorphs of different ages and artificial taxa (morphotype varieties) will be diagnosed on characters of exceptionally wide intrapopulation variability.

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THE CRETACEOUS AMMONITE *EOPACHYDISCUS* AND THE ORIGIN OF THE PACHYDISCIDAE

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ABSTRACT. *Eopachydiscus* Wright, 1955 is confirmed as the earliest, Upper Albian representative of the Pachydiscidae, derived in all probability from a bullate member of the Beudanticeratinae and giving rise to the Cenomanian–Coniacian *Lewesiceras* Spath, 1939. Nuclei of *Eopachydiscus* are ribbed, tuberculate, and constricted, showing even at this stage and date typical pachydiscid ornament; the evolution of *Lewesiceras* simply involved retention of these features into middle growth. The suggestion that the Pachydiscidae arose from *Arrhaphoceras* Whitehouse, 1927 of the Hoplitinae is discounted on morphological, stratigraphical, and biogeographical grounds.

THE family Pachydiscidae Spath, 1922, is among the most important of late Cretaceous ammonites groups, having a cosmopolitan distribution in Turonian to Maastrichtian time. It includes some of the largest and the youngest normally coiled ammonites. In spite of this importance, the early history and origins of the group are ill-documented. In introducing the subfamily Pachydiscinae Spath (1922, p. 120) simply referred to it as 'a subfamily that includes a number of developments of *Puzosinae*'.

Wright (1955, p. 566) noted that the earliest admitted pachydiscid was *Lewesiceras*, and suggested that the earliest species of this genus was the *Pachydiscus* sp. of Pervinqui re (1910, p. 37, pl. 12, figs. 1–3), and that the origins of this genus, and the family, lay in his new genus *Eopachydiscus* (type species *Pachydiscus laevicaniculus* Lasswitz ex Roemer ms., 1904, p. 236, pl. 15, fig. 2; text-figs. 8, 9). Wright also pointed out that *Ammonites brazoensis* Shumard, 1860 (p. 594) was probably an inflated form of the species, and that the poorly known *A. marcianus* Shumard, 1854 (p. 183, pl. 4, fig. 5) might be the inner whorls of the same species, and have priority.

In 1979 Wiedmann and Schneider (p. 667, pl. 9, fig. 6; text-figs. 9A–B) described a new species of *Lewesiceras*, *L. cenomanense*, from the Cenomanian of M lheim-Broich in Westphalia, and suggested that the pachydiscids might be derived from the hoplitid genus *Arrhaphoceras* instead of from unknown desmoceratids.

In order to clarify the origins of this group, we describe below the early development of *Eopachydiscus* on the basis of pyritic nuclei and limestone moulds from the Upper Albian of Texas that in our view confirm its pachydiscid affinities and the desmoceratacean origins of the Pachydiscidae.

SYSTEMATIC PALAEOLOGY

Superfamily DESMOCERATACEAE Zittel, 1895

[*nom. transl.* Wright and Wright, 1951 (ex Desmoceratidae Zittel, 1895)]

Family PACHYDISCIDAE Spath, 1922

[*nom. transl.* Spath, 1923, ex Pachydiscinae Spath, 1922]

Genus EOPACHYDISCUS Wright, 1955, p. 570

Type species. *Pachydiscus laevicaniculus* Lasswitz, ex Roemer ms., 1904, p. 236 (16), pl. 15 (3), fig. 2; text-figs. 8, 9, by original designation = *Ammonites marcianus* Shumard, 1854, p. 183, pl. 4, fig. 5. Upper Albian of Texas.

Diagnosis. Large, rather inflated to compressed, moderately involute. Sides convex, venter more or less narrowly rounded. Nuclei depressed, with primary ribs, bullate or not, and associated constrictions, with or without intercalated ribs. This variable ornament persists into middle growth, when the whorls become progressively higher. Ornament may decline on the body chamber. Suture with broad, open, minutely frilled elements and numerous auxiliaries.

Occurrence. The genus characterizes the '*Eopachydiscus brazoensis*', rightly *E. marcianus*, Zone in the Upper Albian of Texas, and is especially abundant in the Duck Creek Formation in north Texas. It ranges from west Texas/Chihuahua (El Paso-Ciudad Juarez area) up into New Mexico and northern Colorado (W. A. Cobban, pers. comm.). The *marcianus* (= *brazoensis*) Zone is approximately equivalent to part of the European *Mortoniceras inflatum* Zone. Matsumoto (1979, p. 31) has recorded a probable *Eopachydiscus* from the Cenomanian of southern India.

Eopachydiscus marcianus (Shumard, 1854)

Plates 67, 68; text-fig. 1b, c

- 1854 *Ammonites marcianus* Shumard, p. 183, pl. 4, fig. 5.
- 1860 *Ammonites brazoensis* Shumard, 1860, p. 594.
- 1904 *Pachydiscus laevicaniculatus* F. Roemer Manuscript; Lasswitz, p. 236 (16), pl. 15 (3), fig. 2; text-figs. 8, 9.
- 1919 Gateposts and flower bed in Forest Park, built of the large ammonite, *Desmoceras brazoense* . . . Adkins and Winton, pl. 4, fig. 2.
- 1920 *Desmoceras brazoense* (Shumard); Adkins and Winton, pp. 18, 35, pl. 2, figs. 1-2.
- 1920 *Desmoceras* sp. A. Adkins and Winton, p. 35, pl. 2, fig. 3.
- 1923 *Pachydiscus?* sp. Reeside, p. 205, pl. 49, fig. 1.
- 1925 *Desmoceras brazoense* [sic] Winton, pl. 4, fig. 1.
- 1925 *Desmoceras brazoense* (Shumard); Bullard, pl. 20, figs. 1-2.
- 1926 *Desmoceras brazoense* (Shumard); Bullard, pl. 16, fig. 1.
- 1927 *Desmoceras brazoense* (Shumard); Adkins, p. 44, pl. 6, fig. 2.
- 1927 *Desmoceras laevicaniculatum* (Roemer); Adkins, p. 44, pl. 6, fig. 1.
- 1928 *Desmoceras (?) brazoense* (Shumard); Adkins, p. 220, pl. 9, fig. 2.
- 1928 *Desmoceras (?) laevicaniculatum* (Roemer); Adkins, p. 220, pl. 9, fig. 1.
- 1928 *Desmoceras (?) marcianum* Shumard, 1854; Adkins, p. 221.
- 1955 *Pachydiscus laevicaniculatus* Lasswitz ex Roemer ms.; Wright, p. 570.
- 1955 *Desmoceras brazoense* Shumard; Wright, p. 571.
- 1955 *Ammonites marcianus* Shumard; Wright, p. 571.
- 1957 *Eopachydiscus laevicaniculatus* (Lasswitz); Wright, p. L377, fig. 493, 1.
- 1960 *Eopachydiscus brazoense* (Shumard); Perkins, p. 26, pl. 10, fig. 1.
- 1979 *Eopachydiscus marcianus* (Shumard, 1854); Matsumoto, p. 37.
- 1979 *Eopachydiscus laevicaniculatus* (Roemer); Wiedmann and Schneider, p. 667.

Type. The holotype, by monotypy, is the original of Shumard 1854, p. 183, pl. 4, fig. 5, from 'cretaceous strata of Cross-Timbers, Texas'. The specimen has not been traced but the figure, albeit of a poor specimen shows clearly enough the nature of the species at an early growth stage. For further discussion see below (p. 658).

EXPLANATION OF PLATE 67

Figs. 1-16. *Eopachydiscus marcianus* (Shumard, 1854). 1-12, pyritic nuclei. 1, 2, from the Duck Creek Formation on the site of the Denison Dam, Grayson County, Texas, $\times 2$. 3-12, from the same Formation north of Denison, Grayson County, Texas (Renfro Collection), $\times 2$. 13-16, limestone moulds of septate juveniles from the same Formation; 13-14, from USGS locality 17904 on the eastern side of the eastern end of the Sierra Prieta in the Sierra Diabolo Mountains, Texas, $\times 1$. 15-16, from the 'Portland Cement Company strip pit north of Fort Worth, Texas' (ex Renfro Collection), $\times 1$. All specimens are in the U.S. National Museum, Washington D.C.



Description. Nuclei up to 20 mm (Pl. 67, figs. 1–12). The earliest stages visible are smooth and globose. Ornament first appears at a diameter of approximately 2 mm, when the coiling is involute with a deep conical umbilicus and depressed reniform whorl section (Pl. 67, figs. 3, 4). There are five to seven variably developed umbilical bullae per half whorl (Pl. 67, figs. 7, 10, 11). These give rise to single thin or broad distant prorsiradiate and straight primary ribs. These initially die out over the ventrolateral shoulder (Pl. 67, figs. 11, 12), but as size increases they extend, sweeping across the shoulders with a markedly concave course to cross the venter with a distinct convexity (Pl. 67, figs. 8, 9). These primary ribs are associated with a weak to obsolete adapical constriction and a stronger adapertural one (Pl. 67, figs. 1, 8, 9). There may also be shorter, weaker intercalated ribs, arising around mid-flank, a maximum of three between primaries in a specimen 12.5 mm in diameter, five in a fragment with an estimated diameter of 18 mm (Pl. 67, figs. 5, 6). These are most obvious in inflated forms; some less-depressed individuals lack all but a trace of weak intercalatories.

Juveniles 45–160 mm diameter (Pl. 67, figs. 13–16; Pl. 68, figs. 1–11). Our material shows a gap between 20 and 45 mm from the pyritic nuclei to the limestone moulds. The smallest of the latter, however, show a similar range in variation to the former (Pl. 67, figs. 13, 14; Pl. 68, figs. 1–5). The whorl section has become less depressed, and by 45 mm diameter varies from slightly depressed to slightly compressed. The coiling remains involute, with a deep umbilicus. The maximum breadth is at the umbilical bullae or close to the umbilical shoulder with swollen inner and convergent outer flanks and a narrowly arched venter. At one extreme of ornament is the specimen shown in Pl. 67, figs. 13–14, which has distinct distant umbilical bullae that give rise to rounded flexuous ribs, some of which branch from the bulla. These ribs sweep markedly forwards over the ventrolateral shoulders to produce a marked ventral convexity (Pl. 67, fig. 14) and are associated with a strong adapical constriction. There are three to five shorter, weaker, intercalated ribs. With increasing size the umbilical bulla declines, but the inner flank rib strengthens, as does the constriction, to a diameter of at least 100 mm (Pl. 68, figs. 9–11). Other specimens show a predominantly ribbed stage at around 45–90 mm (Pl. 68, figs. 1–8) without conspicuous bullae and with up to nine primaries per half whorl and only one or two intercalatories, leading to individuals like that shown in Pl. 68, figs. 4, 5, where the intercalated ribs have already disappeared leaving an ornament of numerous bar-like flexuous primaries and constrictions. Pl. 68, figs. 6–8 shows a larger, slender specimen of intermediate form with a compressed whorl, many primaries, and weak secondary ribs; Pl. 67, figs. 15–16 shows an even more compressed form with almost obsolete ribs and prominent constrictions.

Adults. This species reaches diameters of almost half a metre and becomes increasingly compressed with a high oval whorl and narrowly rounded venter. Primary flank ribs persist in some (e.g. Adkins 1928, pl. 9, fig. 2) or may disappear before the end of the phragmocone (e.g. Adkins, 1928, pl. 9, fig. 1).

The suture line of a juvenile specimen is shown in text-fig. 1*b*. E is broad and slightly shallower than a broad trifid L, E/L narrow and bifid, L/U₂ asymmetrically bifid with a series of small auxiliaries. A mature suture, shown in text-fig. 1*c*, maintains the same pattern, with intense frilling of both lobes and saddles.

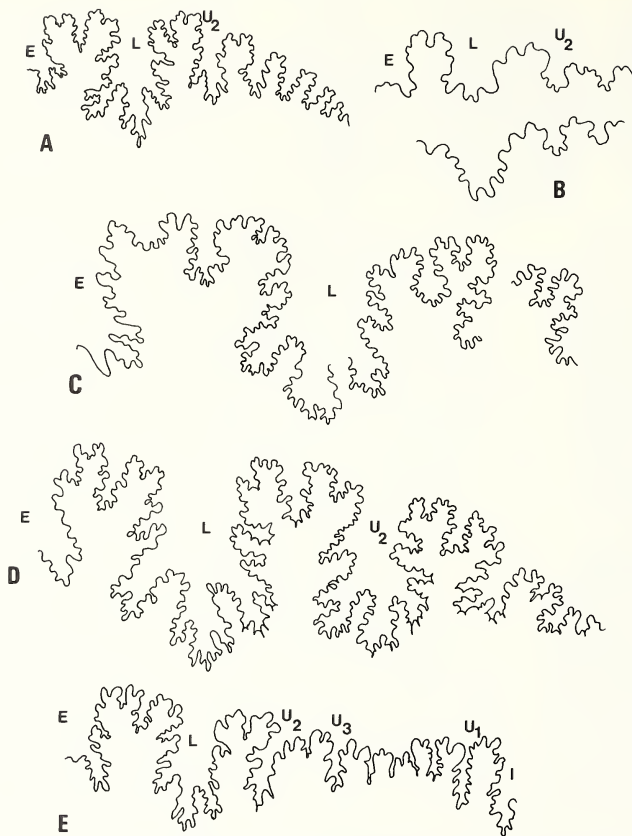
Discussion. *Ammonites marcia* Shumard, the senior name assigned to Upper Albian Duck Creek pachydiscids, was based on a single poorly preserved nucleus less than 30 mm in diameter. Cragin (1893, p. 237) stated 'It is not unlikely that Shumard's *Ammonites marcia* was based on a very young specimen of this species' [*Pachydiscus brazaensis*, Shumard]. Two years later (1895, p. 54 footnote) he considered it identical with *brazaense*. Adkins (1928, p. 221) said that Shumard's figure and description of *marcianum* 'might refer to the juvenile, strongly ribbed form which is widespread in the basal Duck Creek of North-Central Texas and northern Trans-Pecos Texas. The relations of this form to other species are as yet undetermined.' Adkins (1928, p. 220) said of *A. brazaensis* Shumard that 'Shumard's description leaves little doubt as to the identity of this species: his largest individual, in the State Geological Survey (Shumard Survey at Austin was 21 inches in diameter and

EXPLANATION OF PLATE 68

Figs. 1–11. *Eopachydiscus marcia* (Shumard, 1854). 1–3, from the Duck Creek Formation twenty-five miles north of Fort Worth on Highway 81, about one mile north of Rhome, Wise County, Texas (ex Renfro Collection). 4–8, from the same Formation, 'Portland Cement Company strip pit north of Fort Worth, Texas' (ex Renfro Collection). 9–11, Wright's Collection, from the same Formation on Duck Creek '0.6 miles west of Fort Worth–Primrose Road, Tarrant County, Texas' (ex J. P. Conlin Collection). All figures $\times 1$. The originals of figs. 1–8 are in the U.S. National Museum, Washington D.C.



KENNEDY, WRIGHT and CHANCELLOR, *Eopachydiscus*



TEXT-FIG. 1. A, suture of *Uhligella subornata* Casey, 1949 (after Casey 1961, text-fig. 51c), $\times 3$. B-C, sutures of *Eopachydiscus marcianus* (Shumard, 1854); B, from a pyritic juvenile, $\times 12.5$; C, from a limestone mould, $\times 3$. D, *Lewesiceras mantelli* Wright and Wright, 1951 (after Matsumoto 1979, text-fig. 1), $\times 3$. E, *Arrhaphoceras studeri* (Pictet and Campiche, 1860) (after Renz 1968, text-fig. 11a), $\times 3$.

had 10 or 11 broad ribs'. This species is so abundant in the Duck Creek Limestone as to reach rock-forming proportions (e.g. Winton and Adkins 1919, pl. 4, fig. 2; Adkins 1927, text-fig. 4; Perkins 1961, p. 26, pl. 10, fig. 1). All the collections we have seen include both the strongly ornamented form (*A. brazoensis* Shumard) and the feebly ribbed and constricted form (*P. laevicaniculatus* Lasswitz) and this is confirmed by the observations of the late James P. Conlin of Fort Worth (*in litt.*). We

conclude that they are the same species. Conlin (*in litt.*) suggested that the two forms might be dimorphs, but we are unable to confirm this.

The juvenile material described here confirms Cragin's opinion that *marcianus* was the nucleus of the species whose adults were subsequently described by Shumard as *brazoensis*. Despite the poor preservation of the holotype of *marcianus* and the absence of a figure of any of the syntypes of *brazoensis* the evidence of conspecificity is perfectly good and there is no reason not to use the earliest specific name among the three synonyms.

Occurrence. Duck Creek Limestone, Upper Albian, *Eopachydiscus marcianus* Zone and correlatives in Texas, Chihuahua, New Mexico, and northern Colorado.

DISCUSSION

Our redescription of *E. marcianus* shows that the genus *Eopachydiscus* has a typically desmocera-tacean suture and a ribbing style and constrictions that recall the strongly ornamented *Uhligella* Jacob, 1907 (Beudanticeratinae).

Uhligella (see Casey 1961, p. 160 for a discussion of this genus, and text-fig. 1A for a suture) ranges from the Upper Aptian at least to the lower part of the Middle Albian, and is known from western and central Europe, North Africa, and Venezuela, so that it is both chronologically and geo-graphically a potential ancestor.

The link from *Eopachydiscus* to later Pachydiscinae is via *Lewesiceras* Spath, 1939 (see Wright 1979 and Wright and Kennedy 1981 for a review of this genus). The nuclei of *Eopachydiscus* figured here are so similar to the innermost whorls of *Lewesiceras* in whorl section and ornament that the transition between the two involved no more than the retention of the ornament of the young of the former into the middle growth of the latter. The sutures of the two show close similarities (text-fig. 1). The precise line between *Eopachydiscus* and *Lewesiceras* is not known, for the two genera are rare between the low Upper Albian acme of the former and the Lower Turonian acme of the latter. However, Young's specimen of *Lewesiceras* from the Buda Limestone of Cormal County, Texas (Young 1979), the Perviniquière material from the Cenomanian of Algeria (1910, p. 37, pl. 12, figs. 1-3), *Lewesiceras cenomanense* from the Lower Cenomanian of Westphalia (Wiedmann and Schneider 1979, p. 667, pl. 9, fig. 6, text-fig. 9A-B), and Matsumoto's record of *Eopachydiscus* from southern India (1979, p. 31) indicate the persistence of the stock.

Derivations from *Arrhaphoceras*, proposed by Wiedmann and Schneider (1979), presents a number of problems. *Arrhaphoceras* has a suture that is consistently simpler than either *Eopachydiscus* or *Lewesiceras* (text-fig. 1E), never develops constrictions, and has ventrolateral tubercles (see Renz 1968, pl. 2, figs. 20-22; pl. 3, figs. 1-4, 6-11; pl. 4, figs. 1-3). It is also a younger genus than *Eopachydiscus*, clearly linked to the older Hoplitinae of the Old World Boreal realm. These stratigraphic and morphologic criteria are sufficient to eliminate it, in our view. Furthermore, it is difficult to see a group unknown outside the Old World during the late Albian giving rise to *Lewesiceras* which appears in the early Cenomanian of both North Africa and North America.

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THE DIMINUTIVE THECIDEIDINE BRACHIOPOD
ENALLOTHECIDEA PYGMAEA (MOORE)
FROM THE MIDDLE JURASSIC
OF ENGLAND

by P. G. BAKER

ABSTRACT. The discovery of new sources of material has enabled restudy of the minute *Thecideum pygmaeum* Moore, 1861. Although their general organization is close to that of the monoseptal representatives of the Moorellininae the new specimens differ from typical thecideidines in the absence of both dorsal median septum and hemispondylium and in the presence of an incomplete subperipheral rim. The form may prove to be important in tracing the phylogeny of the Thecideidina. It is assigned to a new genus *Enallothecidea* whose characters are considered to be sufficiently distinctive to warrant its inclusion in a new subfamily, the Enallothecideinae.

The species investigated was, prior to the availability of the new material, known essentially from four figures in an account of micromorphic Brachiopoda from the Coral Rag, Lyneham, Wiltshire (Moore 1861, pl. 2, figs. 4-7). It is impossible to ascertain whether type specimens were ever designated. Davidson (1876) disagreed with Moore's (1861) interpretation of specific characters and refigured the species, although whether the new drawings were prepared from Moore's specimens or some of Davidson's own material is not known. Dr. C. H. C. Brunton (pers. comm. 1982) considers that the annotation on Davidson's original drawings, currently housed in the British Museum (Natural History) suggests that Davidson may have redrawn Moore's specimens, although Davidson in his monograph (1876, p. 105) simply refers to specimens 'that passed through my hands'. A tube containing nine specimens was listed as M2852 *Thecideum pygmaeum*, Corallian, when the major part of the Moore collection held in the Bath Literary and Scientific Institution was catalogued by Dr. F. S. Wallis in 1927. Examination of this material shows that the tube in fact contains specimens of *Rioulina ornata* (Moore). No specimens were found in that part of the Moore collection which had been passed on to the Revd. H. H. Winwood (Baker and Copp 1975) and is currently housed in the Somerset County Museum, Taunton Castle. In the absence of the original material, the new specimens must necessarily be compared only with figures; even so their morphology is so distinctive that there can be no doubt that they belong to the same species as that figured by Moore. However, as the species has remained so imperfectly known since its discovery it is here considered necessary to emend the original diagnosis.

Registration of material. The neotype and hypotypes are housed in the British Museum (Natural History) under numbers BB 81112-BB 81114.

Preparation of material. Bulk samples from unconsolidated or only partially consolidated horizons were washed through a nest of sieves. The thecideidines were then hand-picked from dried 350 μm and 175 μm residues under a binocular microscope. Specimens were transferred to glass tubes for further cleaning by weak sonication for periods of up to 10 seconds. Specimens selected for stereoscanning were gold-coated before photography.

SYSTEMATIC PALAEONTOLOGY

Order UNCERTAIN

Suborder THECIDEIDINA Elliott, 1958

Superfamily THECIDEACEA (Gray, 1840) H. and G. Termier, 1949

Family THECIDEIDAE Gray, 1840

Subfamily ENALLOTHECIDEINAE subfam. nov.

Diagnosis. Minute forms with undivided brachial interior, dorsal median septum lacking, lophophore probably trocholophous; hemispondylium not developed. *Age*, Middle Jurassic.

Genus ENALLOTHECIDEA gen. nov.

Etymology. From the Greek *enallōs* (contrary) after the significant departure from typical thecideidine internal morphology.

Diagnosis. Characters of the subfamily.

Type species. *Thecideum pygmaeum* Moore, 1861.

Enallothecidea pygmaea (Moore, 1861)

Plate 69, figs. 1–9; text-fig. 1

1861 *Thecideum pygmaeum* Moore, p. 96, pl. ii, figs. 4–7.

1876 *Thecedium?* *pygmaeum* Moore; Davidson, p. 105, pl. XIII, fig. 16, 16a, b, c.

Type specimens. No holotype designated, syntypes lost. Neotype (here proposed) complete shell BB 81112. Hypotypes, brachial valve BB 81113 and pedicle valve BB 81114.

Dimensions of neotype. Length 0.6 mm, width 0.4 mm, thickness 0.4 mm.

EXPLANATION OF PLATE 69

Stereoscan photomicrographs of *Enallothecidea pygmaea* (figs. 1–9) and other specimens (figs. 10–12) for comparison. All figures are of specimens coated with evaporated gold before photography.

Figs. 11–3. Lateral, brachial, and anterior views of the neotype, BB 81112, $\times 100$.

Fig. 4. Interior of pedicle valve BB 81114 showing the apical attachment scar, the hinge teeth, and the strongly endopunctate shell; the pseudodeltidium is missing in this specimen, $\times 95$.

Fig. 5. Three-quarters profile view of brachial valve BB 81113, rotation and tilt angle 45° , to show the form of the subperipheral rim, the cardinal process (arrowed), and the dental sockets, $\times 90$.

Fig. 6. Interior of brachial valve BB 81113, $\times 105$.

Fig. 7. Near three-quarters profile view of pedicle valve BB 81114, rotation and tilt angle 60° , to show the relationship between the attachment scar and the growth lines, $\times 65$.

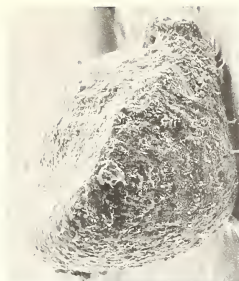
Fig. 8. Posterior view of specimen BB 81114, tilt angle 60° , showing detail of the apical attachment scar, $\times 225$.

Fig. 9. Disturbed secondary shell fabric adjacent to an endopuncta, $\times 2350$.

Fig. 10. Angled view (orientation as fig. 8) of the posterior portion of the pedicle valve of an early juvenile spiriferide, *Howellella* (author's collection, PB 1523), from the Much Wenlock Limestone Formation, Wren's Nest, Dudley, to show the form of the ventral umbonal region prior to the clear differentiation of an interarea, $\times 50$.

Fig. 11. Brachial view of the posterior portion of a pedicle valve of an early juvenile terebratulid, *aff. Plectothyris* (author's collection, PB 1524) from the Oolite Marl, Westington Hill, showing the pedicle collar filling the apex of the delthyrium and the incipient deltidial plates, $\times 80$.

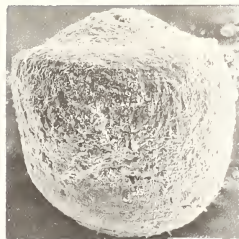
Fig. 12. Brachial view of the posterior portion of a pedicle valve of an early juvenile terebratulid, *Zeilleria* (author's collection, PB 1525), from the Oolite Marl, Westington Hill, showing the beginning of shell resorption at the apex of the delthyrium, $\times 85$.



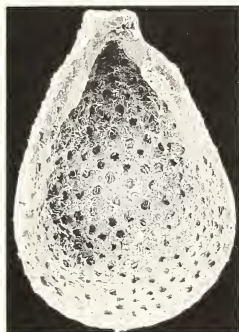
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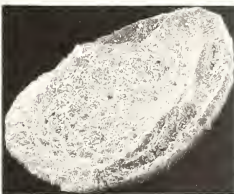
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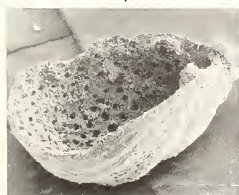
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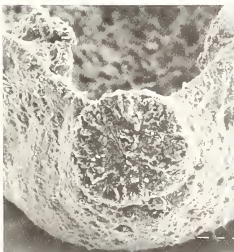
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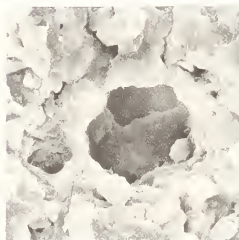
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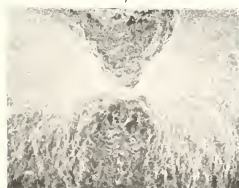
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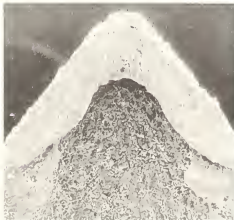
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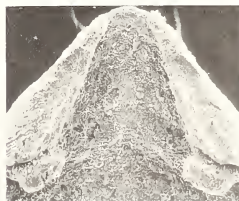
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12

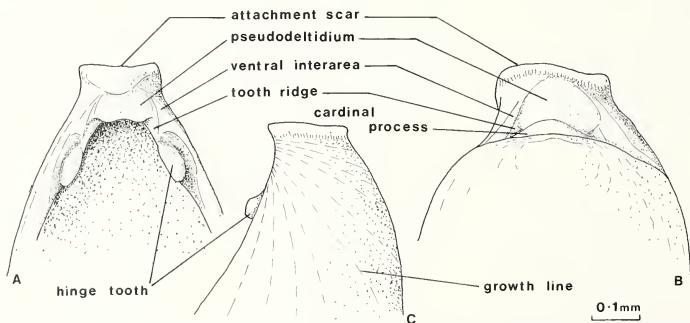
Original diagnosis (Moore 1861). Shell microscopic, longitudinally oval; both valves convex; attached to other bodies at the upper part of the ventral valve; beak slightly produced; area short; deltidium ill-defined. A thin raised ridge passes round the front and sides of the dorsal valve, until it reaches the dental sockets. It is without a central septum, nearly always present in other species, the only ornamentation within the ridge being numerous punctations.

Emended diagnosis. Minute *Enallothecidea*, markedly ventribiconvex, pyriform in outline with a small tuberoso apical attachment scar resulting in a poorly defined ventral inter-area. Pseudodeltidium small, indistinct, and not completely closing the delthyrium anteriorly. Subperipheral rim confined to the lateral and posterolateral regions of the brachial valve, dorsal median septum lacking. Hemispondylium lacking. Shell endopunctate.

Distribution. The locality from which Moore collected his material is given as the Coral Rag, Lyneham, Wiltshire, although the precise horizon from which the specimens were obtained remains unknown. *E. pygmaea* is now known to occur at various horizons at several other localities, e.g. from the Pea Grit (Upper Aalenian, *murchisonae* Zone) at Crickley Hill, grid ref. SO 930 162 near Cheltenham, and from the Oolite Marl (Upper Aalenian, *murchisonae* Zone) at Cleeve Cloud, grid ref. SO 948 261 near Cheltenham, and Westington Hill Quarry, grid ref. SP 142 368 near Chipping Campden, Gloucestershire; also from the Coral Rag (Middle Oxfordian, *tenuiserratum* Zone) at Shellingford Cross Roads Quarry, grid ref. SU 325 940 near Faringdon, and Cumnor Hill Road Cutting (temporary exposure), grid ref. SU 336 954 near Oxford.

Description. External characters. A very small species even by thecideidine standards, reaching a maximum length of only about 0.7 mm, width about 0.5 mm, and thickness about 0.45 mm. The growth pattern of the pedicle valve gives it a distinctive ladle-shaped lateral profile (Pl. 69, fig. 1). The incomplete delthyrial cover means that part of the dorsal surface of the cardinal process remains visible (Pl. 69, fig. 2; text. fig. 1b) when the valves are closed. The pedicle valve began to grow away from the substrate at a very early age so that the area of attachment is always small and apical in position (Pl. 69, figs. 2, 4, 7, 8).

Internal characters. Pedicle valve (Pl. 69, fig. 4). Apart from the cyrtomatodont hinge teeth and strongly developed endopunctuation the interior of the pedicle valve is otherwise featureless. *Brachial valve* (Pl. 69, figs. 5, 6). As previously noted there is no median septum. The valve is characterized only by the typical thecideidine cardinal process, dental sockets, and incompletely developed subperipheral rim. There are no brachial lobes and no suggestion of a bridge but, as in the pedicle valve, strongly developed endopunctuation is present.



TEXT-FIG. 1. Detail of the morphology of the posterior portion of the shell of *Enallothecidea pygmaea*. A, pedicle valve, brachial view. B, complete shell, brachial view. C, pedicle valve, lateral view.

Microstructure. The shell is differentiated into a thin granular primary layer and a fibrous secondary layer (Pl. 69, fig. 9) which most closely resembles the disturbed secondary shell mosaic of moorellinids (Baker 1970, pl. 20, fig. 1).

DISCUSSION

The tuberosc apical attachment scar and growth habit which results in a typical pyriform shape make the exterior of *E. pygmaea* distinctive in its morphology. The species is comparatively rare and apparently local in occurrence. It is probably more common than it appears but, owing to its extremely small size and somewhat unusual appearance, is either usually overlooked or not recognized as a brachiopod. In all cases *E. pygmaea* was found to be associated with coralliferous deposits. The specimens in my collection were all obtained from organo-detrital debris, but Morris (1980) has recovered specimens from unconsolidated residues obtained from small cavities in small reef mounds adjacent to the Crickley Coral Bed at Crickley Hill, suggesting that *E. pygmaea* may have occupied a cryptic niche. Owing to their minute size the possibility that the specimens are juveniles must be considered. Moore (1861) noted the association of *E. pygmaea* with *Rioulina ornata* (Moore) and *R. triangularis* (D'Orbigny) but was unable to relate it to the ontogeny of either species. The same maximum size is attained at all the localities in which *E. pygmaea* has been encountered. Equivalent-sized juveniles of associated small thecideidine species such as *Moorellina granulosa* (Moore) are clearly distinct. There is a remote possibility that the specimens represent juveniles of a hitherto undiscovered adult, but from their apparently localized occurrence and the absence of broken fragments of larger shells this seems unlikely and, in any case, has no bearing on their systematic position.

Because of its minute size Davidson (1876, p. 105) had difficulty in defining the characters of the species and was not completely convinced that it was thecideidine. Pajaud (1970, p. 345) without further discussion dismissed the species as 'non Thécidée'. Fortunately, the ability to study specimens by scanning electron microscopy has enabled the problem to be solved and confirms that the species may be properly assigned to the Thecideidina. The attachment scar, the cardinal process, the cyrtomatodont hinge teeth placed well forwards (Jaanusson 1971), and the secondary shell fabric are characteristically thecideidine. However, the incomplete subperipheral rim, the lack of a hemispondylium, and, more significantly, the lack of a median septum does pose a problem with regard to the systematic position of *E. pygmaea*. Although in many respects it appears to be related to the simple monoseptal forms *E. pygmaea* is the only thecideidine species so far recorded in which a median septum is not developed. As the form of the median septum is currently critical to thecideidine classification (Pajaud 1970) its absence in *Enallothecidea* precludes the possibility of assigning the new genus to an existing subfamily. Throughout the history of the Suborder, representatives of the Thecideidina show the often profound effects of neotenous suppression of characters (Williams 1973). Non-development of a median septum through neotenous suppression may be of phylogenetic significance and the organization of *E. pygmaea* may reflect a condition recognizable in the ancestral stock. Rudwick (1968) and Baker (1970) have suggested a strophomenide ancestry for the Thecideidina. Williams (1973) has argued strongly in favour of a spiriferide ancestor and has shown that a number of characters previously regarded as strophomenide are by no means exclusive to the group. He considers that, as far as the thecideidines are concerned, the cyrtomatodont teeth, the cardinalia, and the shell structure preclude a strophomenide ancestry. Williams does, however, concede the probable importance of cementation, supplemented by the presence of a supra-apical foramen and an entire pseudodeltidium in determining strophomenide affinity. The beak ridges of *E. pygmaea* appear to come together posterior to the attachment scar; also the structure appears to lie ventral to the early growth lines (Pl. 69, figs. 2, 7) so that attachment initially may have been effected by a supra-apical structure. Unfortunately, the minute size of the specimens makes interpretation difficult even with the aid of stereoscan facilities. Care must be exercised as Brunton and MacKinnon (1972) have demonstrated that the supposed supra-apical foramina (Cowen and Rudwick 1966) of *Cadomella*, *Koninckella*, and *Amphiclina* are in fact apical. There is, however, some evidence (Baker

1970, p. 90) that the early juvenile *Moorellina* possessed a pedicle sheath in a supra-apical position. Because of the distorting effect of the attachment scar on the beak area generally, the possibility of a very early apical foramen in *E. pygmaea* should not be discounted.

I previously concluded (Baker 1970) that middle Jurassic thecideidines such as *Moorellina* were probably closely related to *Thecospira*. Work on *Thecospira* (Dagis 1973; MacKinnon 1974, p. 242) subsequently confirmed a remarkable similarity in the shell ultrastructure of the two genera. Dagis argued for a thecospirid ancestor for the thecideidines. It is here considered that this may be a little premature but, in view of what is now known about their shell microstructure, it does seem almost certain that thecospirids are not far diverged from the ancestral thecideidine stock. Both Williams (1973) and MacKinnon (1974) regarding *Thecospira* as a spiriferide anyway, argue for a punctate spiriferide ancestor for the thecideidines. As already noted the pseudodeltidium of *E. pygmaea* is not entire in the strophomenide sense and if one considers the position of the hinge axis (text-fig. 1A), the opening bounded by the tooth ridges should, technically, be regarded as a comparatively large delthyrium closed only in the apical region. Delthyrial covers are already well known among spiriferide brachiopods (Cowen 1968, 1969) and the imbricated delthyrial cover in the small, recently described, *Metriolepis naber* Cooper and Grant (1976) makes the spiriferides an even more inviting proposition as far as the recognition of an ancestral group is concerned. In *E. pygmaea*, if one disregards the distorting effect of the attachment scar, the growth lines of the pedicle umbonal region (Pl. 69, figs. 7, 8; text-fig. 1c) indicate a growth pattern very reminiscent of the ventral umbo of juvenile spiriferides before the inter-area can be clearly defined (Pl. 69, fig. 10). The morphology of the umbonal region of pedicle valve is also superficially similar to that of juvenile terebratulides. However, in view of the profound effects of neotenous suppression of characters it is only to be expected that the ventral cardinalia of juvenile thecideidines will bear some resemblance to the early juveniles of other cyrtomatodont forms. The resemblance is probably most striking when *E. pygmaea* is compared with terebratulidine forms *aff. Plectothyris* (Pl. 69, fig. 11) where a rudimentary pedicle collar is developed very early. It will be noted in the latter, however, that the incipient deltidial plates and the much flatter dorsal surface of the ventral area underline differences in organization probably no less significant than the absence of an attachment scar. Terebratulidine juveniles, e.g. *Zeilleria* (Pl. 69, fig. 12), may be quickly discounted as the apex of the delthyrium is beginning to show signs of resorption even at this early stage of growth. Therefore, the new information regarding the form of the cardinalia in *E. pygmaea* greatly strengthens the argument advanced by Williams (1973) and with which I now concur, notwithstanding the possibility of this species having a supra-apical foramen, that the thecideidines were probably derived from punctate spiriferides. In view of its atypical morphology and potential phylogenetic importance it is here considered that *Enallothecidea* warrants new subfamilial assignment.

Acknowledgement. I thank Mr. P. G. Cooper, Derby Lonsdale College, for help with the preparation of the plate.

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DISTRIBUTION AND AFFINITIES OF THE JURASSIC DASYCLADALEAN ALGA *SARFATIELLA*

by GRAHAM F. ELLIOTT

ABSTRACT. Information on the nature, taxonomy, and stratigraphical and geographical distributions of the dasycladalean algal structure *Sarfatiella* is summarized. It is suggested that *Sarfatiella* is the calcified reproductive structure of an otherwise non-calcified dasycladalean. Its middle Jurassic palaeogeographical distribution is latitudinally wide and believed to have been subtropical as well as tropical.

THE fossil dasycladalean algal structure known as *Sarfatiella* was first figured and discussed, but not named, from the Bajocian of the Corbières, southern France, by Lemoine and Sarfati (1963). Subsequently, it was formally described and figured as *Sarfatiella dubari* by Conrad and Peybernès (1974) from the Aalenian-Bajocian of the Pyrenees. Since then *Sarfatiella* has been recognized as fragments in thin section from many localities (e.g. Radoičić 1976, Elliott 1977, Bassoulet *et al.* 1978). It is frequently assigned with reservation to the structurally similar alga *Cylindroporella*. This paper summarizes certain problems concerning *Sarfatiella*, and discusses its wide and interesting geographical distribution. The specimens studied by me are from England and from Madagascar, and are now in the collections of the British Museum (Natural History).

SARFATIELLA: ANATOMY AND NOMENCLATURE

Sarfatiella shows a central canal or presumed stem-cell cavity, surrounded by successive horizontal whorls, each comprising about eight globular or near-globular 'ampoules' or presumed reproductive cavities, each of these communicating with the stem-cell cavity by a short narrow canal. In the specimens I have examined, the ampoules are crowded and slightly displaced vertically, so making it difficult to count the number per verticil in thin-section. There are no sterile branches preserved, and the ampoules and canals are different in proportions, from sterile branches with associated reproductive structures as seen in many other dasycladalean genera. Calcification in the living plant appears to have originated around individual ampoules and then to have fused to give the cylindrical tubular structure with ampoule cavities within it. Specimens usually show the outer ampoule calcification (peripheral to the cylinder) broken or worn away, presumably a consequence of release of the contents. In *Cylindroporella*, confused with *Sarfatiella* by several workers including myself, and also in *Heteroporella*, the calcified tube contains records of infertile branch systems as well as of fertile ampoules (Bassoulet *et al.* 1978).

The tubes or cylinders of *Sarfatiella* often form the nuclei of superficial ooids or of small oncoids, or they have been worn into clasts. Peybernès (1976) noted their occurrence in this kind of microfacies in the Pyrenees, and this is true also for England (Elliott 1975), and in the Madagascan material available to me.

Clearly these structures are not a record of the whole living plant. It is suggested here that this was a 'conventional' non-calcified dasycladalean, with nucleate holdfast and central stem-cell with successive verticils of sterile side branches, and that before death or seasonal dying down, the upper terminal whorls grew as a calcified reproductive area with the contents being released later. Probably each calcified structure was the terminal portion of a single plant, though it is just possible that there were several to each plant, if it branched like the living *Cymopolia*.

Holosporella from the Thailand Trias (Pia 1930) has been compared with *Sarfatiella* by various authors from Lemoine and Sarfati onwards. Essentially, in the former the very similar calcified ampoules do not communicate with the central cavity, and Pia interpreted it as a calcified 'endospore' structure within the stem-cell cavity of an otherwise non-calcified dasycladalean. Neither his diagrammatic figure nor his other figures show any canals between ampoules and central cavity, and he does not mention them in the text. There is some uncertainty about the Triassic age of the Thailand specimens (Pia 1930, Pia in Narayana Rao and Sripada Rao 1937, and Bassoulet *et al.* 1978, p. 256). *Holosporella* is also known from the Indian Palaeocene (Narayana Rao and Sripada Rao 1937; Pia,



TEXT-FIG. 1. Distribution of middle Jurassic *Sarfatiella* at the present day.

EXPLANATION OF PLATE 70

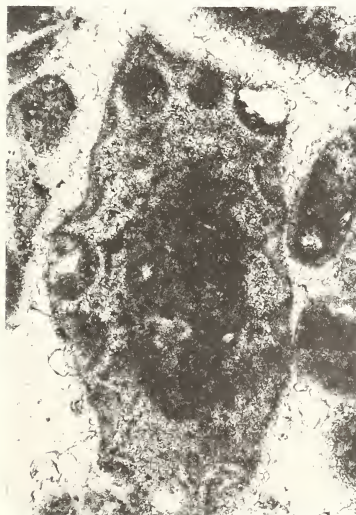
Figs. 1-5. *Sarfatiella dubari*, Conrad and Peybernès. Thin sections $\times 100$; all from Bathonian, middle Jurassic.
 1, longitudinal section; Antankarana, North Madagascar; British Museum (Natural History), Dept. Palaeontology; Reg. no. V.3213a. 2, oblique-longitudinal section; Daglingworth, Gloucester, England; Reg. no. V.57659. 3, oblique-longitudinal section of a *Sarfatiella*-clast; Grandage, Quenington, Gloucester, England; Reg. no. V.60942. 4, transverse section; Antankarana, North Madagascar; Reg. no. V.3213b. 5, transverse section of a *Sarfatiella*-pseudodoid; Daglingworth, Gloucester, England; Reg. no. V.57661.



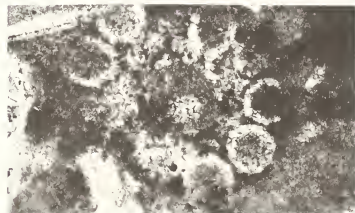
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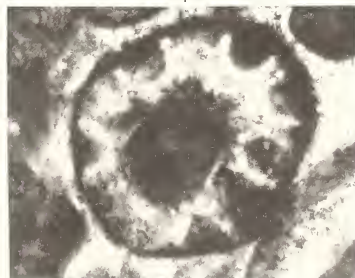
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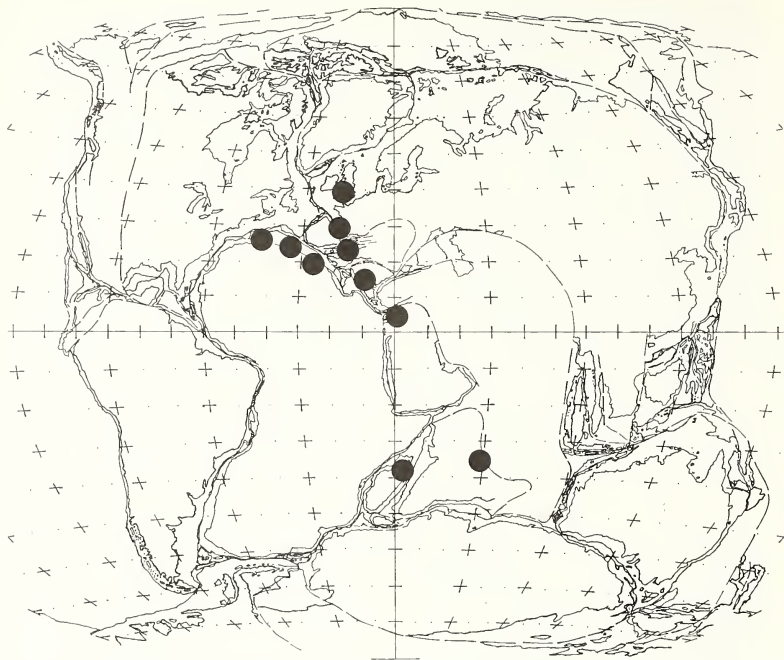
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TEXT-FIG. 2. Distribution of *Sarfatiella*, plotted on a Pangaea continental grouping for the early Mesozoic (Owen 1981).

Narayana Rao and Sripada Rao 1937; Sambe Gowda 1953). Should the type *Holosporella* be found to show communications between ampoules and central cavity it would invalidate Pia's hypothesis and it could affect the validity of the name *Sarfatiella*. The problem is complicated by a qualified record of *Sarfatiella*? from the French Palaeocene (Segonzac 1979). The problems in classifying such dissociated calcified parts of extinct algae are worse still with *Acicularia* s.l., which has even fewer diagnostic characters (ref. Elliott 1981). Bassoulet *et al.* (1979) wisely do not attempt to place *Sarfatiella* in a detailed dasycladalean classification. I follow Bassoulet *et al.* (1978) in using *Sarfatiella* for the middle Jurassic specimens in which the communication pores are often clearly to be seen if sufficient random sections are available. This can be seen both in the French type descriptions, and in English and Madagascan material studied by me.

DISTRIBUTION OF *SARFATIELLA* IN THE MIDDLE JURASSIC

Sarfatiella has been recorded from the middle Jurassic over a wide area. Three accounts summarize this information, containing both original records by the authors themselves and recognition of the genus from previous accounts. These summaries are those of Radoičić (1976), Elliott (1977), and

Bassoulet *et al.* (1978). Where horizons within the middle Jurassic are given, records are of Aalenian–Bajocian, Bajocian, Bathonian, and one of Callovian age. The combined middle Jurassic geographical distribution from these accounts is shown in text-figs. 1 and 2.

It can be seen that not merely does *Sarfatiella* occur at several localities in the tropical western Tethys, where it accompanies the larger and much more conspicuous middle Jurassic *Selliporella*, but the former also extends outside this, north and south of the palaeoequator, to the subtropical areas poor in Dasycladales (see Elliott 1977, 1982). It occurs in the north in the Cotswold district of England, and in the south in Madagascar and Nepal (the latter then south of the Jurassic equator in the present-day Indian Ocean area, on the Indo-Sub-Tibetan Plate).

Sarfatiella in the Jurassic is thus a useful and widespread algal indicator of the Dogger or Middle part of the system. It is to be hoped that the uncertainties over *Holosporella* can be resolved in the future.

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THE JAW APPARATUSES OF CRETACEOUS DESMOCERATID AMMONITES

by KAZUSHIGE TANABE

ABSTRACT. The jaw apparatuses of three late Cretaceous desmoceratin (*Tragodesmoceroidea subcostatus*, *Damesites ainuanus*, and *D. semicostatus*) are described and compared with those of other ammonites and modern cephalopods. The jaws of the three species morphologically resemble one another, and belong to the anaptychus-type jaws of Lehmann (1981), because of the fundamental jaw structures and the absence of a calcareous element. Based on comparison of jaw structures with modern cephalopods and the jaw-muscle relations in modern *Nautilus*, a possible buccal structure of the Desmoceratinae is proposed.

Jaws and a radula have been regarded as primary feeding apparatuses in modern and extinct Cephalopoda. Recently, comparative morphological studies on the jaws of the Ammonoidea have been made successfully in some genera on the basis of well-preserved *in situ* materials (e.g. Closs 1967; Lehmann 1967, 1970, 1971a, b, 1972, 1976, 1979, 1981; Zakharov 1974; Kanie 1982; Kanie *et al.* 1978; Tanabe *et al.* 1980a, b). As a result, it has become clear that the jaw morphology of the Mesozoic Ammonoidea known to us is markedly variable in internal structures, mineralogy, and relative size versus shell size (Kaiser and Lehmann 1971; Lehmann 1976, 1981). Further work on various Mesozoic taxa is, however, required in order to obtain a general idea of the taxonomic and palaeoecological value of ammonite jaws. Most previous work on ammonite jaws dealt with Jurassic material, and little is known on the Cretaceous Ammonoidea other than *Scaphites* (Meek and Hayden 1864), *Scalarites* (Tanabe *et al.* 1980a), *Gaudryceras* and *Tetragonites* (Kanie *et al.* 1978; Kanie 1982; Tanabe *et al.* 1980b).

This paper gives a description of the jaws of three late Cretaceous desmoceratin ammonites on the basis of well-preserved *in situ* specimens from Hokkaido, Japan. A possible buccal structure of the Desmoceratinae is also proposed, relying on comparison with modern *Nautilus*.

MATERIALS

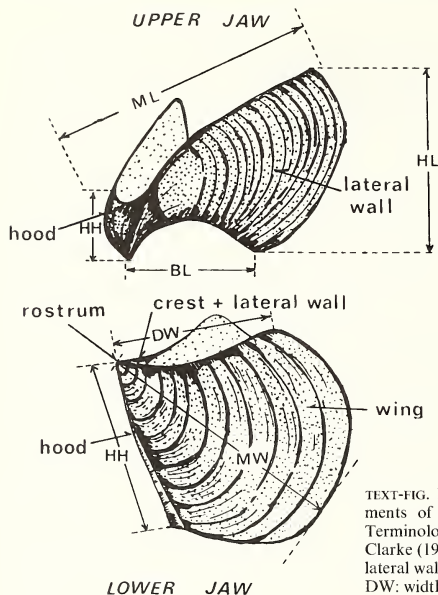
The jaw specimens utilized are: one lower jaw of *Tragodesmoceroidea subcostatus* Matsumoto (GK. H 8064) from the upper Turonian in the lower course of the Abeshinai river, Saku area, northern Hokkaido (lat. 44° 44' N, long. 142° 3' E) (K. Tanabe coll.); one upper jaw of *Damesites ainuanus* Matsumoto (GK. H 8065) in a rolled nodule derived from the middle Turonian in the Gakkonosawa, Saku area (lat. 44° 44' N, long. 142° 1' 30" E) (T. Matsumoto coll.); and a complete jaw apparatus (upper and lower jaws) of *D. semicostatus* Matsumoto (UH. 4545) from the upper Santonian in the Kikumenzawa, a tributary of the Ikushumbetsu river, Ikushumbetsu area, central Hokkaido (lat. 43° 12' N, long. 142° 1' 30" E) (R. Saito coll.). Specimens with prefixes GK and UH are stored in Kyushu University and Hokkaido University respectively.

A 70% alcohol-preserved buccal mass of a male *Nautilus pompilius* Linnaeus, captured off Bindoy, Negros Oriental, the Philippines, was also studied for comparison. The specimen is kept at Ehime University without registered number.

DESCRIPTION

The ammonite jaws examined were found *in situ* within the body chambers, although they have been slightly removed from their original position during fossilization (Pl. 71). As they are all preserved in calcareous nodules, a three-dimensional reconstruction of jaw morphology is possible on the basis of comparison with modern cephalopod jaws.

Concerning recognition of upper and lower jaws, I follow Lehmann's (1970) definition, relying on the mode of occurrence of jaws and radula within the body chamber in life position. The morphotype with a wide, concave outer lamella in the jaw specimens examined is regarded as comprising lower jaws, because of the essential similarity in gross morphology to Lehmann's (1970) anaptychus-type lower jaws. The morphotype consisting of a pair of wide inner lamellae and a short reduced outer one, is compared with the upper jaws of most previously known ammonites (Meek and Hayden 1864; Lehmann 1970, 1971a, 1972, 1975, 1976, 1981). Text-fig. 1 shows the basic morphology and measurements of the reconstructed desmoceratid ammonite jaws.



TEXT-FIG. 1. Basic morphology, terminology, and measurements of desmoceratid ammonite jaws (lateral views). Terminology is that applied to modern coleoid jaws by Clarke (1962). BL: length of base, ML: maximum length of lateral wall, HH: height of hood, HL: height of lateral wall, DW: width of wing, MW: maximum length of wing.

Suborder AMMONITINA Hyatt, 1889
 Superfamily DESMOCERATACEAE Zittel, 1895
 Family DESMOCERATIDAE Zittel, 1895
 Subfamily DESMOCERATINAE Zittel, 1895
 Genus DAMESITES Matsumoto, 1942
 Upper jaw of *Damesites ainuanus* Matsumoto

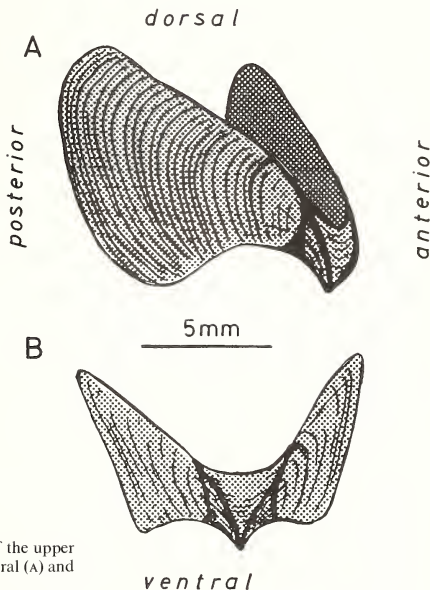
Plate 71, fig. 2a-c; text-fig. 2

The upper jaw bearing shell of *D. ainuanus* attains 30 mm in diameter, although it lacks the majority of the body chamber. The upper jaw is preserved near the base of the body chamber (Pl. 71, fig. 2a). It is made up of a pair of wide inner lamellae (lateral wall without crest region) and a reduced short inner lamella (hood). These lamellae are combined one with another in the anterior rostral region. The jaw lamellae are composed of dark-coloured homogenous material only. They are thickest in the anterior portion, and become thinner toward the

posterodorsal margin. The rostrum projects strongly ventrally, like a parrot's beak. A V-shaped depression is present along the median line of the outer lamella. The open angle between the paired inner lamellae is about 30° . The inner and outer lamellar surfaces are sculptured with regularly spaced, concentric undulations (numbering more than twenty) and fine striae respectively.

Measurements (cf. text-fig. 1)

ML	HL	HH	BL	HL/ML
13.75 mm	10.02 mm	3.45 mm	10.02 mm	0.73



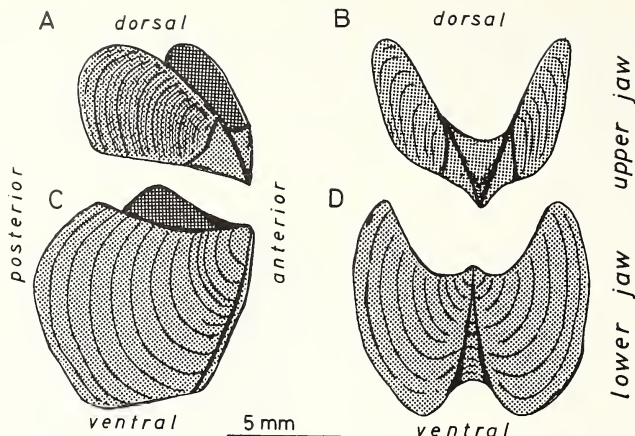
TEXT-FIG. 2. Three-dimensional reconstruction of the upper jaw of *Damesites ainuanus*. GK. H 8065. Left lateral (A) and anterior (B) views.

Jaw apparatus of *Damesites semicostatus* Matsumoto

Plate 71, fig. 1a-d; text-fig. 3

Complete upper and lower jaws are preserved in the middle part of the body chamber of an immature *D. semicostatus* (29.65 mm in maximum shell diameter with an almost perfect body chamber). The lower jaw was formerly interpreted by Nagao (1932) as an operculum, but I have recently found an upper jaw on the posteroventral side of the lower (Pl. 71, fig. 1a). The mode of occurrence shows that both jaws have been moved slightly from their original position.

Upper jaw. The upper jaw is similar in fundamental morphology to that of *D. ainuanus*. It differs, however, from the latter in having a less projected rostrum, smaller lateral wall height in relation to maximum lateral wall size (see LH/ML in the measurements), and more widely spaced, less numerous concentric undulations on the inner lamellar surface. Furthermore, unlike *D. ainuanus*, the paired inner lamellae possess more than ten radial striae on the posterodorsal margin. The open angle formed by the paired lateral walls is acute (c. 40°) as in *D. ainuanus*.



TEXT-FIG. 3. Three-dimensional reconstruction of the jaw apparatus of *Damesites semicostatus*. UH. 4545. Left lateral (A, C) and anterior (B, D) views of the upper (A, B) and lower (C, D) jaws.

Lower jaw. The lower jaw may consist of widely developed outer and reduced short inner lamellae, although the greater part of the latter are coated with host rock. In all probability the two lamellae are united in the anterior rostral region. The outer lamella is gently convex anteriorly, and there is a prominent radial groove along the hood, dividing the outer lamella into two wing areas. The open angle between the two wings is about 50° . The outer lamellar surface is ornamented with more than twenty regularly spaced concentric undulations.

The upper and lower jaws are not much different in size, as shown by the following measurements.

Measurements (cf. text-fig. 1)

	ML	HL	BL	HH	HL/ML	ML/shell diam.
Upper jaw	11.00 mm	6.15 mm	9.30 mm	2.65 mm	0.56	0.37
	MW	DW	HH	HH/DW	MW/shell diam.	
Lower jaw	11.15 mm	9.35 mm	10.85 mm	1.16	0.38	

Genus TRAGODESMOCEROIDES Matsumoto, 1942

Lower jaw of *Tragodesmocerooides subcostatus* Matsumoto

Plate 71, fig. 3a-c; text-fig. 4

EXPLANATION OF PLATE 71

Fig. 1. Jaw apparatus of *Damesites semicostatus* Matsumoto. UH. 4545. 1a, mode of occurrence of upper (uj) and lower (lj) jaws within the body chamber, $\times 1$. 1b, c, right lateral (b) and dorsal (c) views of the upper jaw, $\times 2$. 1d, right lateral view of the lower jaw, $\times 1$.

Fig. 2. Upper jaw of *Damesites ainuanus* Matsumoto. GK. H 8065. 2a, mode of occurrence within the incomplete body chamber, $\times 1$. 2b, c, right lateral (b) and anterior (c) views, $\times 2$.

Fig. 3. Lower jaw of *Tragodesmocerooides subcostatus* Matsumoto. GK. H 8064. 3a, mode of occurrence near the aperture, $\times 1$. 3b, c, anterior (b) and left lateral (c) views, $\times 1.7$.

All specimens whitened.

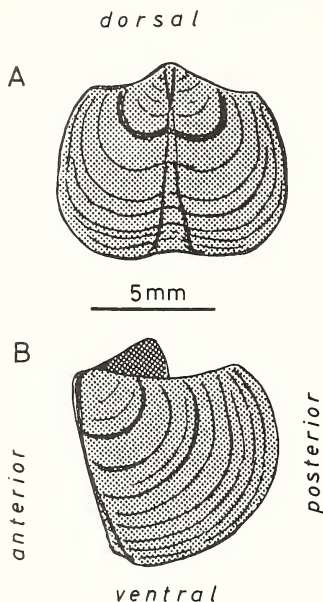


TANABE, Cretaceous ammonite jaws

A lower jaw was found near the aperture of an immature shell 26.9 mm in maximum shell diameter. It is characterized by the gently convex, wide outer lamella. An inner lamella is not well exposed in the present specimen, but it may be reduced, as in *D. semicostatus*. The outer lamella is divided into two wing areas by a prominent groove running along the hood. The surface of the lamella is sculptured with many regular-spaced, concentric undulations. The gross morphology and surface ornament of the lower jaw of the present species are, therefore, essentially similar to those of *D. semicostatus*, but it is distinguished by the more strongly projected rostral edge. Furthermore, the lower jaw in relation to the shell diameter of this species is smaller than that of *semicostatus*.

Measurements (cf. text-fig. 1)

MW	DW	HH	HH/DW	MW/shell diam.
8.60 mm	7.60 mm	7.75 mm	1.02	0.25



TEXT-FIG. 4. Three-dimensional reconstruction of the lower jaw of *Tragodesmocerooides subcostatus*. GK. H 8064. Anterior (A) and right lateral (B) views.

COMPARATIVE MORPHOLOGY

On the basis of differences in the internal structures and mineralogy, Lehmann (1981) classified the complete jaw apparatuses of fifteen ammonite genera known to us into the following three morphotypes: (1) anaptychus (= normal) type, represented by such Palaeozoic and Mesozoic genera as *Eoastanites*, *Olenekites*, *Psiloceras*, and *Dactylioceras*; (2) aptychus type, which is characterized by some Jurassic and Cretaceous genera (e.g. *Eleganticeras*, *Hildoceras*, *Scaphites*, and *Scalarites*); and (3) calcified anaptychus type (= rhynchaptychus type of Lehmann *et al.* 1980), which is probably restricted to Mesozoic Lytocerataceae and Phylloceratina (Tanabe *et al.* 1980b).

As described above, the jaw apparatuses of the three desmoceratines examined resemble one another in basic morphology and surface ornament. This fact suggests to us that jaw morphology is taxonomically stable in the Desmoceratinae. Judging from the fundamental jaw structures and the absence of a calcified element, the jaws of the three species apparently belong to the anaptychus-type of Lehmann (1981). They are, however, slightly different from the typical anaptychus-type jaws of Jurassic *Psiloceras*, *Arnioceras*, and *Pleuroceras* (Lehmann 1970) in the larger upper jaws in relation to the lower ones and the presence of a distinct median depression in the lower jaws. As such a median depression is also observed on the inner chitinous layer of all aptychus-type lower jaws (Lehmann 1972, 1976, 1981), the lower jaws of the Desmoceratinae correspond to an intermediate form between the typical anaptychus-type jaws and the aptychus-type jaws.

The fossil record of aptychi and anaptychi (Trauth 1927–1936) suggests that most Palaeozoic and Triassic Ammonoidea possessed an anaptychus-type jaw apparatus (Lehmann 1976, 1981). In the early Jurassic aptychus-type jaws first appear in some genera of the Ammonitina, and throughout the Jurassic and Cretaceous they have been specially adapted in many groups of the Ammonitina and Ancyloceratina (Lehmann 1976, 1981). In contrast to this, anaptychus-type jaws are rare in occurrence in the middle Jurassic to Cretaceous. This paper is the first reliable record of Cretaceous ammonites with anaptychus-type jaws. Moreover, the lower jaws of the early Cretaceous Haplocerataceae, a possible ancestor of the Cretaceous Desmocerataceae (Wright 1981), are represented by the form genera lamellaptychi and laevilamellaptychi (Trauth 1927–1936), both of which are included in the aptychus-type lower jaws of Lehmann (1976, 1981). From these lines of evidence, it is probable that the jaws of the Desmoceratinae evolved in a different way from the anaptychus-type jaws of the early Jurassic Ammonitina.

Comparison with modern cephalopod jaws shows that the upper jaws of *Damesites semicostatus* and *D. ainuanus* somewhat resemble those of modern coleoids (especially of octopods) in having a beak-like rostral edge and a reduced short outer lamella (hood). They are, however, clearly distinguished from all modern cephalopod upper jaws, because the inner lamella is distinctly divided into two lateral walls.

The lower jaws of *D. semicostatus* and *Tragodesmoceroideis subcostatus* are more similar to those of modern *Nautilus* than coleoids in the presence of a widely developed, convex outer lamella (wing and hood) and a short reduced inner lamella (crest and lateral wall). But they do not possess an anterior calcified element (conchorhynch), which is present in the Nautilida and in Lytoceratid and phylloceratid ammonite lower jaws (Müller 1974; Saunders *et al.* 1978; Tanabe *et al.* 1980b). The surface ornament pattern on the upper and lower jaws of the desmoceratines examined is essentially like those of modern cephalopods.

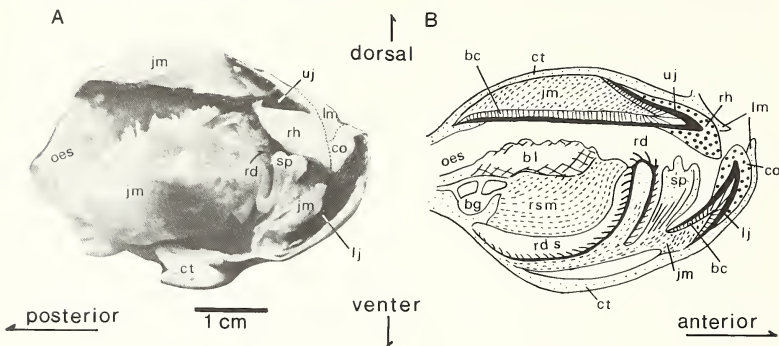
RESTORATION OF BUCCAL STRUCTURE

It is well known that in the modern Cephalopoda the jaw apparatus is present within a buccal mass. The buccal mass of cephalopods includes jaw plates, radula, jaw and radular support muscles, buccal palp, salivary papilla and oesophagus (Young 1977). Both upper and lower jaws are connected with strong jaw muscles for biting or cutting up food.

The mode of occurrence of the upper and lower jaws-radula association within the body chambers of some Jurassic ammonites (Lehmann 1967, 1971a, 1972, 1979) strongly suggests that the jaws and radula in the Ammonoidea were present within a buccal mass, as in all modern cephalopods. Details of the buccal structures in the Ammonoidea, however, have long been uncertain. The reason for this owes much to the lack of knowledge about the structural relationship between jaw plates and muscles. Kanie (1982) recently speculated on possible jaw-muscle relations in the Cretaceous tetragonitid ammonites, relying on comparison with the muscular system of modern *Nautilus*. However, he showed no concrete evidence of the muscles of either ammonites or *Nautilus*.

More recently, Tanabe and Fukuda (1983) proposed detailed buccal structures in a late Cretaceous *Gaudryceras* (Lytoceratina) on the basis of the comparative histological observations of the chitin-secreting cell impressions on the jaw surface of the ammonite and modern cephalopods. As Dilly and

Nixon (1976) have already realized, in modern Cephalopoda a layer of chitin-secreting cells (beccublast cells) is intercalated between the hard tissue of the jaws and jaw muscles. Tanabe and Fukuda (1983) made clear that the beccublast cells and jaw muscles are only present in the outer side of the upper jaw and/or the inner side of the lower jaw in *Sepia* and *Nautilus*. The other sides of the jaws are, therefore, free from muscles and are directly covered with a connecting tissue. Text-fig. 5 shows such jaw-muscle relations in modern *Nautilus*.



TEXT-FIG. 5. Buccal structure of *Nautilus pompilius*. A, photograph of the median-sectioned buccal mass. Ehimé University specimen from off Bindoy, Negros Oriental, the Philippines. B, Diagram showing the internal organs of a buccal mass. uj, upper jaw; lj, lower jaw; rh, rhyncholite, co, conchorhynch; jm, jaw muscles; bc, beccublast cells; rd, radula; rds, radular sac; rsm, radular support muscles; bl, lateral buccal palp; sp, salivary papilla; bg, inferior buccal ganglion; lm, labial margin; oes, oesophagus, ct, connecting tissue. Terminology from Young (1965, 1977).

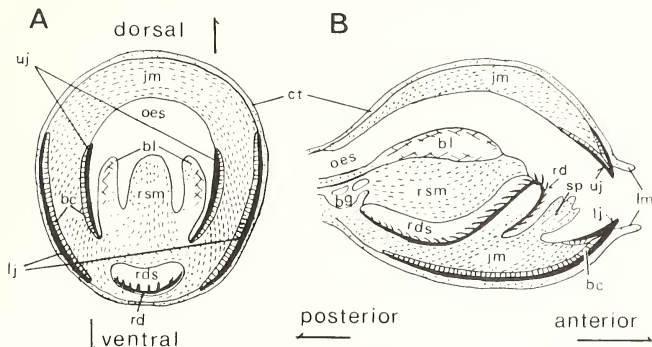
Tanabe and Fukuda (1983) reconstructed a modern *Nautilus*-like jaw muscular system in *Gaudryceras*, on the basis of the restriction of beccublast cell imprints to the inner side of the lower jaw.

As already described, the lower jaws of *D. semicostatus* and *T. subcostatus* examined are essentially similar to those of *Nautilus* and *Gaudryceras*, except for the absence of an anterior calcified element, the conchorhynch. Furthermore, the outer side of the lower jaws of the two desmoceratines is ornamented with numerous concentric growth rings, as in *Nautilus*. From this indirect evidence, it is postulated that in the Desmoceratinae the jaw muscles and beccublast cells were connected with the inner side of the lower jaw.

In all modern cephalopods the inner lamella of the upper jaw is formed of a strongly convex, single chitinous layer, unlike that of the desmoceratines (Clarke 1962). The outer side of the upper jaws of modern cephalopods are wholly covered with fairly thick jaw muscles with intercalated beccublast cells (Young 1965, 1977; Tanabe and Fukuda 1983). Although there is no concrete evidence for the upper jaw-muscle relations in the Desmoceratinae, the outer surface of the paired inner lamellae was probably covered with jaw muscles, as in all modern cephalopods. In the desmoceratines examined the inner lamella of the upper jaws is distinctly divided into two separated lateral wall areas in the posterior region. This fact means a reduction of muscle attachment area on the upper jaws. It is therefore reasonable to deduce that in the Desmoceratinae the mechanical properties of jaw muscles in the side of the upper jaw might be weaker than those of the lower jaw. In connection with this problem, Lehmann (1981) pointed out that in most Mesozoic ammonites the upper jaws are more or less smaller than the lower ones. In all probability in the Mesozoic Ammonoidea which possessed

aptychus- or anaptychus-type jaws, the lower jaws might have functioned more actively for feeding than the upper jaws.

In conclusion, a buccal structure of the Desmoceratinae is proposed in text-fig. 6.



TEXT-FIG. 6. Diagram showing presumed buccal structure of a desmoceratine ammonite, based on comparison with the buccal structure of modern *Nautilus*. Cross (A) and median (B) sections. For abbreviations see explanation of text-fig. 5.

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Cover: The Lower Liassic (Jurassic) oyster *Gryphaea arcuata incurva* J. Sowerby, 1815, from Gloucestershire, England; known popularly as 'The Devil's Toenail'. Specimens in the National Museum of Wales.

EVOLUTION AND FUNCTIONAL MORPHOLOGY OF THE CYSTOID *SPHAERONITES* IN BRITAIN AND SCANDINAVIA

by C. R. C. PAUL and J. F. BOCKELIE

ABSTRACT. The directly attached diploporite cystoid *Sphaeronites* is characterized by a closely approximated mouth and anus on an oral platform, and densely developed diplopores. Three subgenera are recognized: *Sphaeronites* s.s. (lower Ordovician, Sweden); *Peritaphros* (middle and upper Ordovician, Britain, Norway, Sweden, Baltic States); *Ataphros* subgen. nov. (upper Ordovician, South Wales). Early species occur in 'Sphaeronites beds' with few other echinoderms. Later species are less abundant, but occur with a more diverse echinoderm fauna. *Sphaeronites* shows evolutionary trends towards increased plate thickness and plate size (hence reduced number of plates per theca), increased anal area (and inferred food processing capacity), and decreased diplopore density. Diplopore structure also evolved. Those of *Sphaeronites* s.s. are deeply sunken with blunt spines on the rims; *Peritaphros* diplopores have a large central tubercle surrounded by a moat-like channel but no rim spines; *Ataphros* diplopores have just the central tubercle. Changes in diplopores have been investigated using computer programs to simulate respiratory gas exchange. The larger, less densely packed diplopores of later species achieved the same respiratory capacity, but with individually more efficient diplopores. Reconstructions of the soft tissue cover of diplopores confined to the moat-like channels of *Peritaphros* or covering the central tubercle as well, yielded respiratory capacities 10% and 100% of *Sphaeronites* s.s. The maximum calculated evolutionary increase in saturation with O₂ of body fluids occurred with soft tissue covers 20 μ m thick. It is inferred that these covers were 10–50 μ m thick in life. Calculation of food processing capacity suggests that *Sphaeronites* could gather all the food they could metabolize with simple, unbranched appendages (?brachioles) of a length equal to the thecal diameter. Computer programs offer a powerful tool in reconstructing unpreserved parts of fossils essential to functional interpretations.

Sphaeronites is revised systematically. Nine species are recognized of which one is left under open nomenclature and the following are new: *S. (Sphaeronites) minor*, *S. (Peritaphros) pauciscleritatus*, *S. (P.) variabilis*, and *S. (Ataphros) insulporus*.

SPHAERONITES was a directly attached diploporite cystoid genus which survived throughout the Ordovician from the Arenig to the Ashgill and is found in Britain, Scandinavia, and the Baltic States. It is type genus of the family Sphaeronitidae and superfamily Sphaeronitida. The type species of *Sphaeronites*, *Echinus pomum* Gyllenhaal, 1772, was one of the first two cystoids ever described. Historically and taxonomically *Sphaeronites* is an important genus. In this paper we revise the genus, document its evolutionary trends, and show that *Sphaeronites* is also very important in an evolutionary context.

We first became interested in the genus independently, in the course of revising British (CRCP) and Norwegian (JFB) Ordovician cystoid faunas, respectively. Also independently, we realized that the Swedish cystoid figured by Regnéll (1945, pl. 15, fig. 1) as 'Gen. & sp. indet.' was a new species of *Sphaeronites*. On discovering our joint interest we combined to revise the genus thoroughly in Britain and Scandinavia, considering its stratigraphical and geographical occurrences, functional morphology, mode of life, and evolution. Paul (1972, 1973) had already documented an evolutionary trend in diplopore density, and the functional significance of this trend has been investigated quantitatively using computer programs to simulate gas exchange. As a result of this study we recognize eight named species, four new, in three subgenera, one new. The evolutionary trend in diplopore density achieved the same respiration rate with progressively fewer, but individually more efficient, diplopores. Computer-generated quantitative estimates of respiration rates have also enabled us to reconstruct some unpreserved parts of the fossils, namely the cover of the diplopores and feeding

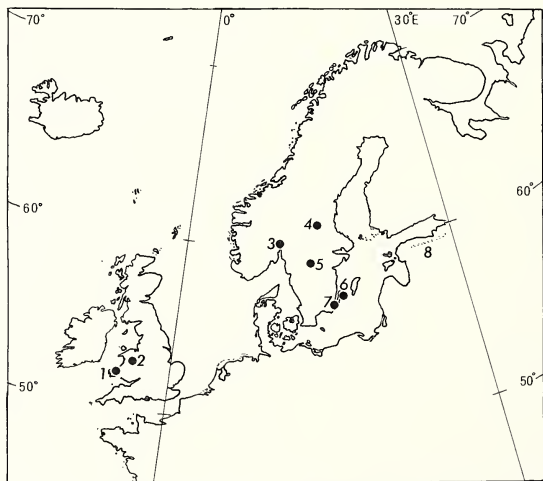
organs, with more certainty than was previously possible. Computer models offer a powerful tool in the study of functional morphology in extinct groups of fossils such as the cystoids. Since this study is largely concerned with the evolution of *Sphaeronites*, we consider first its geographical and stratigraphical occurrence, in order to establish the sequence of species.

OCCURRENCES

The principal localities for *Sphaeronites* are illustrated in text-fig. 1. All are Ordovician and range in age from upper Arenig to middle Ashgill. Correlation of *Sphaeronites*-bearing horizons is presented in text-fig. 2. Stratigraphical information on specific localities is given below, while palaeoecological information is given later. The localities discussed here provide the best evidence for the ages of the species which can be attributed to *Sphaeronites* as we understand the genus. The reasons for accepting only these species within the genus *Sphaeronites* are discussed in the systematic section.

Shoeshook, near Haverfordwest, Dyfed, South Wales (loc. 1, text-fig. 1). Paul (1973, fig. 5), presented a section through the Shoeshook Limestone together with known occurrences of cystoids, including *S. litchi* (Forbes). Price (1973, 1980) has discussed the trilobite fauna and correlation of the Shoeshook Limestone. In the later paper Price considered that at the type locality the Shoeshook Limestone ranges in age from low Ashgill, zone 2 possibly up to zone 5 (i.e. Cautleyan to Rawtheyan). The enigmatic diploporite described as 'Incertain sedis sp. D' (Paul 1973, p. 61) has since been found to represent a new species of *Sphaeronites*, *S. (Ataphros) insuliporus*, known only from the Shoeshook Limestone. Both species appear at almost the same level, between 11 and 13 m, and disappear at the same level, about 37 m in the section. *S. (P.) litchi* is also known from the Rhiwlas Limestone which is Rawtheyan (Ashgill, zone 5).

Rhiwlas and Llwyn-y-Ci, near Bala, Gwynedd, North Wales (loc. 2, text-fig. 1). Bassett *et al.* (1966, p. 252) report a total thickness of 6.4 m of Rhiwlas Limestone at the type section. The fauna indicates a middle Rawtheyan age according to Bassett (*in Williams et al.* 1972, fig. 5). *S. puriformis* (Forbes) is not uncommon in



TEXT-FIG. 1. Map of north-west Europe showing the principal localities for *Sphaeronites*. For details of localities, see text.

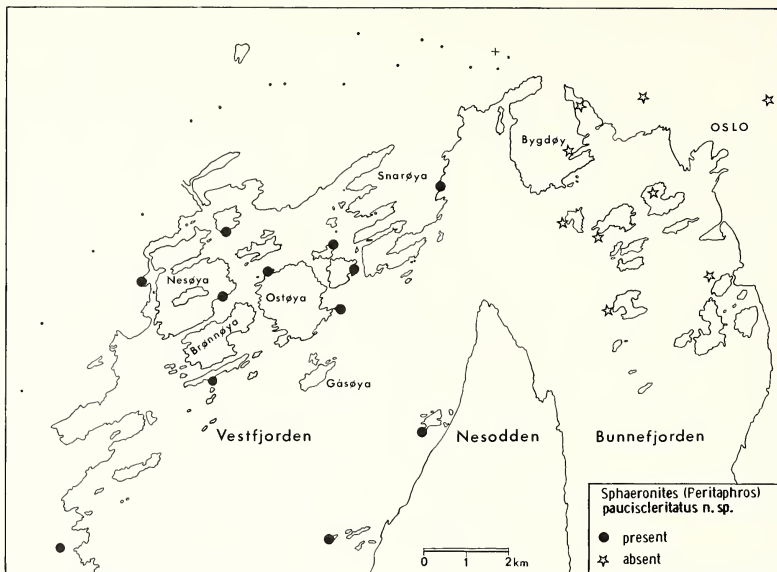
SERIES	British stages	Graptolite zones	Oslo-Asker Stages	South & Central Sweden Stages	WALES	NORWAY	SWEDEN
Ashgill	Hirnantian	?	Calc. sandstones	Boda Imst.	Tommarp	S. (P.) lichi - ■■■■ S. (P.) pyriformis ■ S. (A.) ■ S. (P.) pauciscleritatus ■ 	

TEXT-FIG. 2. Correlation diagram showing stratigraphical ranges of the species of *Sphaeronites* dealt with in this paper.

old collections from Rhiwlas Manor and Llwyn-y-Ci (locs. 6/1 and 6/3 of Paul 1973, p. 8). We have collected about ten more specimens from loose blocks which once formed the walls of the old Ffryddan Factory.

Asker and Bærum, Norway (loc. 3, text-fig. 1). *S. pauciscleritatus* sp. nov. occurs commonly in a 1 m band in the middle of the lower Chasmops Limestone (Stage 4b β), a sequence with approximately 50% limestone nodules and 50% shale. The lower Chasmops Limestone probably correlates with the Soudleyan-Longvillian boundary (middle Caradoc). Even though the lithologies have a wide geographical distribution (Størmer 1953), *S. pauciscleritatus* has a limited occurrence on the mainland and islands west of Oslo (Asker and Bærum districts, text-fig. 3) in what may have been an area of shallower water (Bockelie 1978, p. 199, fig. 3A).

Siljan district, Sweden (loc. 4, text-fig. 1). Two or possibly three species of *Sphaeronites* occur at different horizons within the Siljan district. Only one, *S. variabilis* sp. nov., is reasonably common and confined to Dalarna, while the stratigraphical positions of the other two are better established elsewhere. *S. variabilis* occurs at Osmundsberget as the commonest species in a prominent cystoid bed about 10 cm thick and lying approximately 5 m below the top of the Fjäckå Shale within the Slandrom Limestone. It also occurs as scattered specimens through the lower Jonstorp Limestone and into the crinoidal calcarenite flank facies of the Boda Limestones up to about 24 m above the top of the Fjäckå Shale. In the southern section of Osmundsberget quarry, where the *S. variabilis* band was best exposed in 1974, Ordovician limestones occur at least to 78 m above the Fjäckå Shale so that *S. variabilis* is confined to the lower third or less of the Boda Limestone. At Skälberget, nearby, *S. variabilis* occurs from 5 to 36 m above the Fjäckå Shale and the Ordovician limestones are estimated to be 75 m thick above the Fjäckå Shale. While precise thicknesses may not be reliable as most beds thin rapidly away from Boda mound cores, it does seem reasonably established that *S. variabilis* occurs from just below the Fjäckå Shale up into the lower part of the Boda Limestone, but not to the top. This corresponds to a range from somewhere in the Pusgillian up to the Cautleyan or possibly low Rawtheyan, but certainly not into the



TEXT-FIG. 3. Map showing localities for *Sphaerionites (Peritaphros) pauciscleritatus* sp. nov. in the Oslo Region, Norway. Note its absence from the more north-easterly outcrops.

Hirnantian as previously suspected. *S. variabilis* is recorded from a number of other Boda carbonate mounds in Dalarna, but the precise range of the species is unknown at these localities.

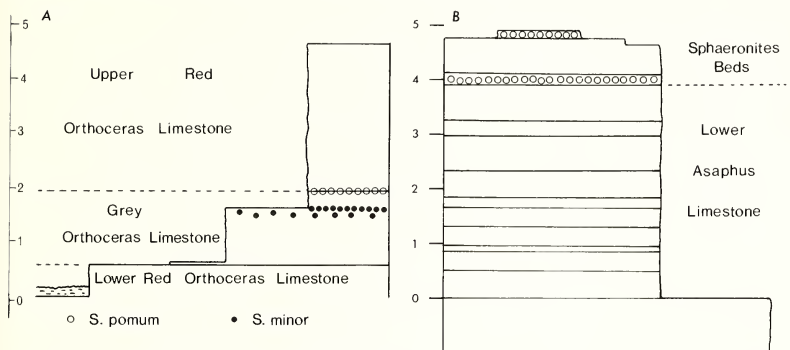
Kinneulle, Västergötland, Sweden (loc. 5, text-fig. 1). In the quarries at Österplana on the east side of Kinneulle Mountain (and elsewhere around the Mountain) a section is exposed from the lower Red Orthoceras Limestone through the Grey Orthoceras Limestone into the upper Red Orthoceras Limestone (text-fig. 4A). *S. pomum* (Gyllenhaal) occurs in a discontinuous band at the junction between the Grey and upper Red limestones while *S. minor* sp. nov. occurs in a continuous band 16–20 cm lower down within the Grey Orthoceras Limestone and scattered specimens occur to at least 15 cm below this band. The Grey Orthoceras Limestone probably correlates with the upper Arenig or lowermost Llanvirn. Irrespective of precise age, *S. minor* is undoubtedly older than *S. pomum* and both species maintain their relative positions to within 2 cm all around Kinneulle Mountain.

Bödahamn, Öland, Sweden (loc. 6, text-fig. 1). *S. globulus* occurs in the Dalby Limestone north of the new harbour at Bödahamn. It ranges through perhaps 20 cm of limestone associated with *Caryocystites dubia* (Angelin), *Lophocystis granatum* (Wahlenberg), and *Echinospaerites aurantium* (Gyllenhaal). The Dalby Limestone probably correlates with the middle Llandeilo to lowermost Caradoc.

Södra Möckleby, Öland, Sweden (loc. 7, text-fig. 1). At the top of the upper level of the huge quarry at Södra Möckleby two beds of *S. pomum* occur separating the lower and upper Asaphus Limestones (Moberg 1890). The upper *Sphaerionites* bed is up to 5 cm thick and crops out on the surface above the top of the quarry face (text-fig. 4B). The lower *Sphaerionites* bed is approximately 75 cm lower down and up to 20 cm thick. Both beds yield only *S. pomum* (we have found no *S. minor* outside Kinneulle), often weathered so as to reveal beautifully the details

of the surface and diplopores (e.g. Pl. 72, figs. 1, 2). The *Asaphus* Limestones correlate with the upper Arenig or lower Llanvirn, but the age of these *Sphaeronites* relative to those of *S. pomum* and *S. minor* at Kinnekulle cannot be determined exactly on present knowledge.

Estonia and Leningrad Province, U.S.S.R. (loc. 8, text-fig. 1). *S. globulus rossicus* has been named from Ordovician outcrops in the east Baltic by Hecker (1964, pl. 4, figs. 3, 4a, b). Prof. Hecker intends to describe this form together with another new species. As we have no specimens for comparison, we cannot relate them morphologically or stratigraphically to the other species considered here.



TEXT-FIG. 4. Sections at Österplana, Kinnekulle, Västergötland (A), and at Södra Möckleby, Öland (B), showing occurrences of *Sphaeronites* spp. At Österplana *S. (S.) pomum* occurs at the junction between the Grey and Red Orthoceras Limestone, with *S. (S.) minor* some 20 cm lower. At Södra Möckleby two beds with *S. (S.) pomum* occur at the top of the quarry section. No correlation is implied by the relative positions of the sections. Scales in m.

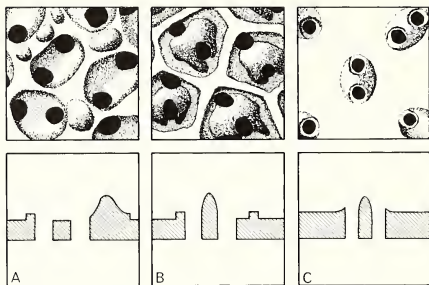
We consider the first occurrences of species to be more important in an evolutionary context than the total range. On this basis the species of *Sphaeronites* which we have studied evolved in the following order: *S. minor* preceded *S. pomum* in the upper Arenig or lower Llanvirn. *S. globulus* (upper Llandeilo-lower Caradoc) and *S. pauciscleritatus* (middle Caradoc) followed in the middle Ordovician, while *S. variabilis* (Pusgillian-?Rawtheyan) followed by *S. litchi* and *S. insuliporus* (Cautleyan-Rawtheyan and Cautleyan, respectively) and finally *S. pyriformis* (Rawtheyan) came last in the Ashgill. This sequence differs slightly from that indicated previously (Paul 1972, 1973) in that *S. variabilis* is now known to occur below the Fjäckå Shale and not to extend up into the highest Boda Limestone. Previously it had been thought to occur only in the Boda Limestone and to range from the upper Ordovician into the lowermost Silurian (e.g. Regnéll 1945). This species fits better into the evolutionary trend in diplopore density as a low Ashgill rather than a high Ashgill form. In discussing all evolutionary trends, the above order of species is considered to reflect the actual course of evolution. However, we have relatively little information about *S. pyriformis*, so many comparisons between early and late species contrast *S. minor* with *S. litchi* as the latest species for which reasonable numerical data are available.

MORPHOLOGY, TERMINOLOGY, MEASUREMENTS

Sphaeronites was a directly attached diploporite cystoid with a cylindrical to spherical theca. A distinct attachment area is present on most specimens and the mouth and anus lie close together on

a raised oral platform. Between these larger orifices and to the left is a small circular gonopore, usually 0.5 mm in diameter. In *S. pauciscleritatus* a minute oval hydropore occurs just adoral to the gonopore.

The arrangement of thecal plates in *Sphaeronites* is not fixed, except in the oral area, and most species seem to have added plates during growth. In *S. pauciscleritatus* and *S. variabilis* the usual seven circum-oral (CO, plural COO) plates, found in all genera of Sphaeronitidae (Paul 1973, p. 12), occur but only the six larger circum-oral, which form the frame of the peristome, have been confirmed in other species. All plates bear numerous diploporos which are densely and evenly packed over the entire theca, except the attachment area and oral platform. In *S. pomum* and *S. pauciscleritatus* a narrow marginal band free of diploporos may occur on some thecal plates.



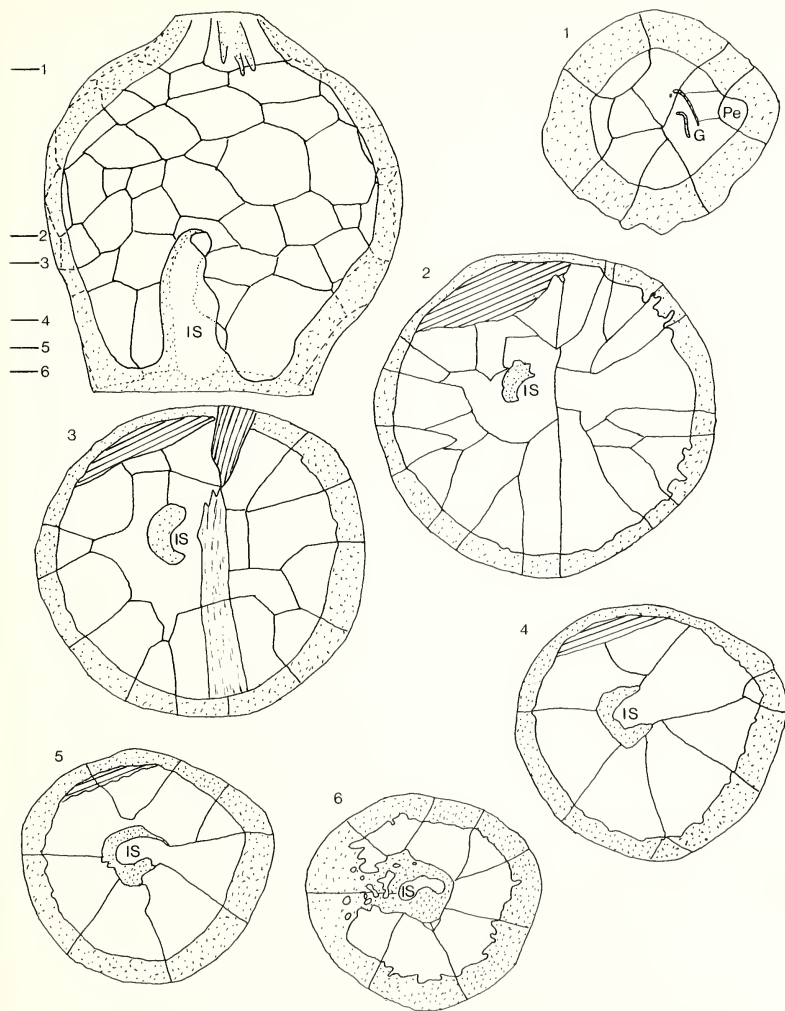
TEXT-FIG. 5. Typical diploporos of subgenera *Sphaeronites* s.s. (A), *Peritaphros* Paul (B), and *Ataphros* subgen. nov. (C).

Two types of diploporos have been used to recognize two subgenera (Paul 1973, pp. 20–21). In *Sphaeronites* s.s. there are sunken peripores and conspicuous tubercles or short spines developed on the peripore wall (Pl. 72, fig. 1; Pl. 73, fig. 6; text-fig. 5A), while in *Peritaphros* a large central tubercle develops and the peripore is reduced to a moat-like channel around the central tubercle (Pl. 73, fig. 7; text-fig. 5B). A third type of diploporos is now known to occur in the Sholeshook Limestone species *S. (Ataphros) insuliporus* subgen. et sp. nov., where only the central tubercle of *Peritaphros* remains and the peripore has become so reduced as to be absent altogether (Pl. 73, fig. 8; text-fig. 5C). So far *S. (A.) insuliporus* is the only known species of *Ataphros* and it is exceedingly rare.

The mouth of *Sphaeronites* lies within an oval or rounded peristome and was covered with six palatal plates in life. The anus opened through a polygonal periproct covered by a simple anal pyramid of five to seven anal plates which could open outwards but not inwards. Both orifices lie very close together on the oral platform and rarely exceed 3 mm in major dimension. Nearly always five ambulacra, each with one to three small ambulacral facets, are developed adjacent to the mouth on the oral platform. Four examples of *S. variabilis* are known in which ambulacrum III is undeveloped. Three ambulacral facets occur in ambulacrum II and III of the holotype of *S. pauciscleritatus*, necessitating a slight modification of the diagnosis of the genus *Sphaeronites* given by Paul (1973, p. 19). As with almost all Diploporita, the ambulacral appendages which articulated on these facets are never preserved.

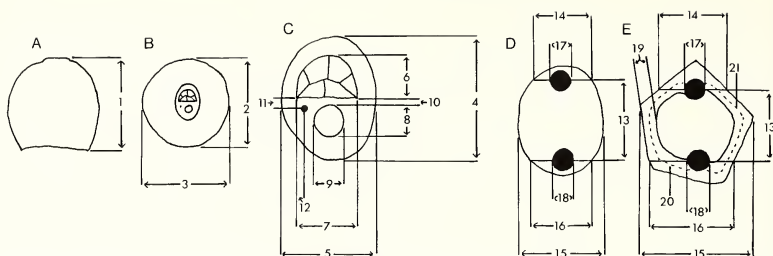
Attachment was direct and the size and shape of the attachment area were largely controlled by the available substrate. *Sphaeronites* only exceedingly rarely developed an aboral stem-like extension to the theca. Of the thousands of specimens we have seen, only one or two show such a feature.

Within the theca an internal hollow spine has been detected in *S. variabilis* (text-fig. 6), *S. litchi*, *S. globulus* and *S. pauciscleritatus*, all species of the subgenus *Peritaphros*. It is absent in all examples of *Sphaeronites* s.s. that have been sectioned, but may well have been characteristic of *Peritaphros*.



TEXT-FIG. 6. Reconstruction of half a serially sectioned specimen of *Sphaeronites (Peritaphros) variabilis* sp. nov. (top left) to show internal spine (IS). 1-6, six transverse sections to show gonoduct (G), periproct (Pe) and internal spine. Positions of sections indicated at top left. Stereom stippled, calcite fill white, sediment ruled.

Broken lines in section 3 indicate damage during cutting. Approximately $\times 2.5$.



TEXT-FIG. 7. Diagram showing principal measurements used in computer programs and descriptions. A and B, measurements taken from whole thecae; C, measurements of oral platform; D, measurements of dipopores of *Sphaeronites* s.s.; and E, of subgenus *Peritaphros*. Measurements are: 1, thecal height; 2, 3, thecal diameters (mean thecal diameter is taken as the average of all three); 4, 5, length and width of oral platform; 6, 7, length and width of peristome; 8, 9, two diameters of periproct; 10, separation of peristome and periproct; 11, 12, positions of gonopore with respect to peristome (gonopore diameter was also recorded where possible); 13, perpendicular canal separation (taken as length of dipopore); 14–16, three widths of dipopores, one at each perpendicular canal and the maximum width perpendicular to the axis (dipopore width taken as the average of all three); 17, 18, perpendicular canal diameters; 19, width of peripore canals in *Peritaphros* spp.; 20, 21, approximate length of peripore canals in *Peritaphros* spp.

The measurements made of the theca, oral area, and dipopores of *Sphaeronites* are indicated in text-fig. 7.

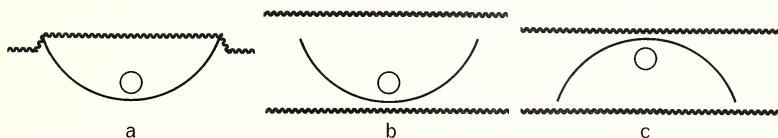
PRESERVATION

British and Scandinavian *Sphaeronites* mostly occur in three types of sedimentary rocks, all of which were probably formed in shallow seas. In Sweden, *Sphaeronites* spp. occur in bedded limestones, often in countless numbers forming distinct *Sphaeronites* beds, as at Kinnekulle, Västergötland, and on the island of Öland. *S. variabilis* occurs in bedded limestones and in the flank facies of the Boda Limestone mounds, in Dalarna, Sweden, although in smaller numbers. In contrast to these carbonate deposits, Welsh and Norwegian *Sphaeronites* occur in clastic sediments with only a small proportion of associated carbonate. The preservation of *Sphaeronites* and associated fauna varies with these different rock types.

Bedded limestones. *S. minor* and *S. pomum* occur in countless numbers in two distinct horizons which probably extend all around Kinnekulle Mountain and are almost continuously exposed for 2 km between Österplana church and Sveningstorp. All specimens lack ambulacral appendages, which are unknown in all species of *Sphaeronites* (and all but a few species of *Diploporita*), and most lack oral and anal cover plates. Tests are largely filled with sediment and randomly orientated within the beds. A few show geopetal infills of sparry calcite above sediment. In both *Sphaeronites* beds, examples can be found with geopetal infills dipping in random directions at high angles to bedding. Further field evidence of reworking is shown by the orthoconic nautiloids, most of which have excentric siphuncles and are preserved with the siphuncle below. Many orthocones have only half the shell preserved and are truncated against discontinuity surfaces, which are very common in the section. However, several examples of half orthocones can be found convex up, or concave up but not truncated against a discontinuity surface (text-fig. 8). Orthocones show strong preferred orientation at several horizons, with V and T orientations indicating currents from the north.

Thin sections reveal that both the *minor* and *pomum* beds at Österplana are largely biomicrite which may be matrix or grain supported. The commonest fossil fragments are of echinoderms and trilobites, but ostracodes, brachiopods, and gastropods occur as well. Sediment fills within cystoids are often of fine micrite with very few small fossil fragments, but more complex fillings can be seen, with fine micrite followed by sparry calcite, or

occasionally fine micrite followed by grain-supported biomicrite with common sparite replacements and cavity fills. Where *Sphaerionites* are preserved epifaunal on other *Sphaerionites*, no interlocking of stereom occurs and all evidence suggests that substrate specimens were dead and at least partly sediment filled before attachment of epifaunal specimens. One sectioned specimen shows geopetal fills parallel to the attachment surface and has excellently preserved surface topography, suggesting that it was buried *in situ*, but with so many randomly orientated tests, chance alone would account for a single example preserved the right way up. The evidence of winnowing, reworking, and current activity suggests very slow net accumulation of sediment which has been further reduced by compaction and pressure solution. Some of the discontinuity surfaces represent contemporaneous hardgrounds, or at least firm grounds, and very rarely crinoid attachment discs encrust directly on to the surfaces, but no other hardground indicators have been seen. The *Sphaerionites* beds seem to represent lag deposits with the distinct possibility that later individuals were epifaunal on rolled and reworked earlier individuals.



TEXT-FIG. 8. Diagram showing relationship of orthocones to discontinuity surfaces in the *Orthoceras* Limestone at Österplana, Kinnekulle, Västergötland, Sweden. Most orthocones are preserved with the siphuncle below and the upper edges truncated against discontinuity surfaces (a). A few show the relationships in (b) and (c) demonstrating that the incompleteness of the orthocones is not entirely due to the discontinuity surfaces. In (b) the orthocone was only partly buried and the upper part decayed before renewed sedimentation. In (c) the resulting half shell was overturned before final burial. This preservation implies very slow sedimentation rates and the section has since been further reduced by pressure solution along the frequent discontinuity surfaces. We believe the discontinuity surfaces are partly original, but have been enhanced by pressure solution, as is clearly the case in (a). All three drawn from field sketches.

Other echinoderms include fairly common *Bolboporites*, and a cheirocrinid rhombiferan with disjunct pectinirhombs, with a hybocrinid crinoid and *Rhipidocystis* which are rarer. All of these are represented by isolated plates only. Other fauna, like the other echinoderms, is sparse except for orthocones. Trilobites, gastropods, brachiopods, and ostracodes are evident. The slow accumulation of sediment implies that these two *Sphaerionites* species were less abundant when alive than they are now. Nevertheless the relative rarity of other fauna suggests they were genuinely very common and gregarious.

At Södra Möckleby, on Öland, *S. pomum* occurs alone in two similar *Sphaerionites* beds about 60 cm apart. Here again orthocones are very common and show strong preferred orientation indicating currents from the north. In section most orthocones are complete and show randomly positioned siphuncles. Only a few examples are truncated by discontinuity surfaces, which are common in this section too. The upper surfaces of both *Sphaerionites* horizons have rare crinoid attachment discs on them, again suggesting at least firm ground development. The overlying Viruan (middle Ordovician) is close to the top of the section, perhaps only 30 cm above the upper *Sphaerionites* band, which suggests that both *S. pomum* horizons in Öland may be younger than the bed at Kinnekulle.

Thin sections reveal that the lower *Sphaerionites* bed is a grain-supported biosparite with a little, possibly original, micrite, while the upper horizon is grain- or matrix-supported biomicrite very much like the beds at Kinnekulle. Spar-filled *Sphaerionites* are more common in the lower bed which is thicker and has cystoids with better preserved surface details. Specimens in the upper unit are often incomplete, abraded, or otherwise damaged. Epifaunal *Sphaerionites* are more common in the upper bed and, as at Kinnekulle, they apparently grew on dead, rolled, and sediment-filled substrate specimens. In one example, the stereom of the epifaunal specimen partly penetrated two of fourteen diplopore canals in the section, the other twelve being sediment filled. No interpenetration of stereom has been seen.

Associated echinoderms include a hemicosmitid and a cheirocrinid Rhombifera, crinoid stems, and *Bolboporites*. Other fauna include orthocones, trilobites, brachiopods, and ostracodes. Crinoid columnals and

brachials are more common and varied than at Kinnekulle, but otherwise the fauna is similar. Again net sediment accumulation was probably slow, but the *Sphaerionites* were genuinely very common.

S. globulus occurs with three other cystoid species in the Dalby Limestone at Bödahamn, Öland. Both the echinoderm and other fauna are more abundant and varied than in either of the lower Ordovician localities described above. Vertical sections cannot be seen as all the outcrop is on the foreshore. *S. globulus* and *Echinospaerites aurantium* are usually spar filled, while *Lophotocystis granatum* and *Caryocystites dubia* are more commonly sediment filled. Apart from these complete cystoids, *Bolboporites*, a cheirocrinid, and various crinoids are represented and the non-echinoderm fauna includes trilobites, brachiopods (articulates and rare inarticulates), bryozoans, gastropods, rare bivalves, ostracodes, conulariids, and ortho- and gyroconic cephalopods.

Thin sections show the Dalby Limestone to be a grain-supported biomicrite with common sparite-filled voids varying to grain- or matrix-supported biomicrite. The rare *S. globulus* with sediment fill have much finer biomicrite fill than the surrounding matrix. Sediment fills in other cystoids show several stages of development, including matrix-supported fine-grained biomicrite and grain-supported coarser biomicrite. The exact sequence is not clear, but occasionally fills show 'graded bedding' of fossil fragments within a micrite matrix. As elsewhere, many cystoids have suffered pressure solution and have lost their surface ornament above and below, but may retain it in a peripheral band. Again sediment accumulation seems to have been intermittent and slow with cystoids common and gregarious, but the fauna is no longer dominated by a single species.

The only other '*Sphaerionites* bed' we have examined is a discontinuous bed which is now apparently quarried away, but which was formerly well exposed on the south side of the uppermost level of the quarry at Osmundsberget, Dalarna, Sweden. Here *S. variabilis*, *Heliocrinites ovalis*, and possibly a *Caryocystites* species occurred in profusion in 1974.

Thin sections reveal a matrix-supported biomicrite with some clay admixture often concentrated in discontinuity surfaces which truncate cystoid tests and crinoid columnals. Cystoids are partly filled with sediment and partly spar filled. Geopetal surfaces parallel the bedding, and evidence for current activity and reworking is absent. Some sediment fills within cystoids are graded and show multiphase filling. Associated fauna is dominated by echinoderm debris.

All these bedded limestone occurrences of *Sphaerionites* have some features in common. They are in markedly bioclastic sediments, usually with a micrite matrix. The *Sphaerionites* are common to abundant and were apparently gregarious in life. Two slightly different modes of preservation occur from which we infer slightly different preservational histories. All specimens were epifaunal when alive; most became detached at, or soon after, death and all lost the ambulacral appendages. Where the oral and anal cover plates were also lost or where the test itself was damaged, sediment fill was coarse-grained, often grain-supported, and nearly or totally complete. Where the cover plates were retained, sediment fill was fine and often very incomplete, being followed by spar fill growing in optical continuity with test plates and forming so-called 'crystal apples'. Both types may have been reworked, but generally where contemporaneous reworking occurred cover plates were lost and spar-filled specimens are less common. The conclusion that cover plates were usually lost by reworking seems inescapable. Finally, most specimens have suffered some pressure solution and secondary spar infilling of the organic spaces in the stereom during diagenesis.

Flank facies of carbonate mud mounds. Above the Fjäckå Shale in Dalarna, *S. variabilis* occurs in the equivalents of the Lower Jonstorp Formation beneath the Boda Limestone and also in the flank facies through the lower half or so of the Boda Carbonate mounds. The Lower Jonstorp at Skälberget consists of thinly bedded limestones with a greater or lesser clastic content. In thin section, lithologies vary from muddy, matrix-supported biomicrite to grain-supported and pressure-welded echinoderm biosparites with clastic accumulations in solution-compaction horizons. Small angular quartz grains are not uncommon in the clastic concentrations. Sutured contacts between echinoderm grains abound in the echinoderm debris limestones. At Osmundsberget the Lower Jonstorp is very similar and at both localities the alternations of clastic rich and echinoderm-rich limestones strongly resemble the flank facies of the Boda mounds except that they lack original dip. The flank facies consist of thin (1–5 cm) echinoderm debris limestones which alternate with reddish-brown or green shales. *S. variabilis* occurs in both the limestones and the shales. The specimens are randomly orientated but retain the oral and anal cover plates and are hence largely spar filled. *S. variabilis* accompanies a rich cystoid fauna including *Caryocystites ovalis* (Angelin), *Heliocrinites stellatus* Regnéll, *Eucystis angelini* Regnéll, *E. raripunctata* (Angelin), *E. quadrangularis* Regnéll, and *Haplospira oblonga* (Angelin). The accompanying non-cystoid fauna is also abundant and includes brachiopods, trilobites, bryozoans, occasional corals and gastropods, ostracodes, crinoids, and calcareous algae at some horizons. Most cystoids have complete tests although the *Eucystis* spp. characteristically have lost their cover plates. All these species are directly attached

forms and lived on the flanks of the mounds. We suspect that crinoid meadows occurred higher up the mounds and, on death, contributed to the flank limestones, possibly following storms. Wherever and whenever suitable substrata stabilized the cystoids colonized them. On death of the cystoids, which may have been caused by sudden influxes of mud that now forms the shale horizons, the cystoids were disturbed and probably rolled downslope slightly, but were otherwise undamaged. Geopetal infills indicate original dips on the flank facies of up to 20° or more. Diagenetic changes again appear to be limited to secondary infilling with spar and some pressure solution, but bitumen-impregnated specimens occur rarely at Osmundsberget and large cubes of secondary pyrite occur in some flank limestones.

Although *S. variabilis* occurs in the flank facies of the Boda Limestone, it appears first in bedded limestones. It occurs through several metres of the Lower Jonstorp Formation before making its appearance as isolated specimens or at most clusters of several tens of specimens in the flank facies. *Haplosphaeronis* and *Eucystis* occur in thousands in some flank deposits and it is reasonable to infer that even *S. variabilis* was not primarily associated with bioherms. A single example of *S. globulus* has been collected from the flank facies of the Kullberg Limestone mound at the type locality, Kullberg. Again it occurred in a *Haplosphaeronis* bed with thousands of specimens, but no other *Sphaeronites* is known associated with carbonate mound structures.

Clastic sediments. *S. pauciscleritatus* occurs in a fine-grained clastic sediment with limestone nodules in the middle of Stage 4b β of the Oslo Region, west of Oslo. Oral and anal cover plates are preserved in some individuals which tend to be largely calcite filled. Other fills include a fine-grained argillaceous micrite and 'coal blende' (asphalt), as a dark crystalline filling. A small proportion of angular silt-grade quartz is present plus some finely divided pyrite. The rock is not very fossiliferous in thin section, but some rare trilobite and echinoderm stem fragments occur. In the rock orthid brachiopods, trilobites (*Chasmops*), ostracodes, and bryozoans, including *Diplotrypa*, have been found. Locally, large, loose thecal plates of a cheirocrinid cystoid occur. The sediment is usually full of *Chondrites* burrows, a situation commonly found in the fine grained sediments of the Oslo Region. Most of the material of *S. pauciscleritatus* seems to be randomly distributed in the sediments (one to three specimens per square metre). None of the specimens was still attached, but the shape of the attachment area suggests that some of them may have been epifaunal on orthoconic cephalopods, and later became detached. The presence of oral and anal cover plates and the size range (20–50 mm diameter) of *S. pauciscleritatus* suggest that the individuals were not transported very far and that final burial occurred relatively soon after death. *S. pauciscleritatus* only occurs in a restricted area which correlates with the occurrence of fine quartz. It may well have been associated with local N.-S. trending topographic highs in the Oslo Basin (Bockelie 1978).

S. litchi and *S. insuliporus* occur in the Sholeshook Limestone in South Wales. At Sholeshook, the Sholeshook Limestone is about 50 m thick, although the top and bottom cannot be seen. The lower part consists of muddy siltstone with perhaps as much as 20% angular silt-grade quartz, which alternates with fine argillaceous limestones in which the quartz content is reduced. Ferroan calcite occurs as fine crystals and fills veinlets. All indications are that it is secondary, and that when deposited the Sholeshook Limestone contained very little carbonate other than fossil fragments. Passing up the section, the grain size of the quartz increases, together with fossil content and pyrite. Pyritized echinoderms are not uncommon in the upper part of the section. The pyritization is a very early diagenetic phenomenon and tends to fill the organic spaces in the stereom meshwork of the inner portion of the plates only. The detailed structure of the stereom is revealed under suitable weathering (Paul 1971, pp. 9–11). Diagenesis which affects only the inner portion of thecal plates is not uncommon in cystoids. In general, it is confined to very early effects in complete thecae. Quite possibly decay of the soft tissue within a complete theca created a different chemical environment which triggered these diagenetic effects. Recent echinoids from Florida show similar post-mortem effects including growths of calcite crystals on the inner surface of the test (but nowhere else), which perhaps formed within a week of death.

In the upper Sholeshook Limestone, mica and small rock fragments are found above about 30 m in the section and the rock becomes a subgraywacke. Irregular burrows, probably *Chondrites*, occur throughout the section and are indicated by a darker filling than the surrounding rock. Associated cystoid fauna is abundant and varied. *Haplosphaeronis multifida* dominates, accounting for perhaps half the known specimens, but at least a dozen other species occur. Non-cystoid fauna is equally rich. Price (1973) records forty-one species of trilobites. Brachiopods, bryozoans, corals, ostracodes, cephalopods, and conulariids make up the rest of the fauna.

Most of the *Sphaeronites* specimens are randomly orientated and sediment filled. However, some are calcite filled and the cover plates are preserved on at least one example we have collected (Pl. 72, fig. 4). Reworking has occurred in the upper part of the Sholeshook Limestone. Paul (1973, pl. 10, fig. 1) illustrates one specimen of *H. multifida* which was reworked, rolled, and abraded, after initial burial and complete filling of the test with a little sediment and then sparry calcite. Laterally, the thecal plates are entirely worn away, exposing the calcite

fill within, and the specimen was redeposited as a small pebble. Much of the cystoid fauna in the upper Sholeshook Limestone may have undergone a similar two-stage burial history, with initial burial *in situ* followed by exhumation and redeposition nearby. Although approaching a graywacke, the Sholeshook Limestone shows no features of turbidite deposition.

North of Bala, North Wales, *S. pyriformis* occurs in the Rhiwlas Limestone which varies from a grain-supported clastic biomicrite to a muddy limestone with small strings of fossil debris. Current activity is evident and ferroan calcite occurs patchily through the rock and as overgrowths on echinoderm ossicles. Pressure welding is obvious in the grain-supported microfacies. A little angular silt-grade quartz occurs.

S. pyriformis is always sediment filled, the cover plates are unknown, and it occurs with a rich fauna of echinoderms and other fossils. At least ten other species of cystoids occur in the Rhiwlas Limestone, and Whittington (1968, p. 119) records twenty-nine species of trilobites. *S. pyriformis* is always small (10–15 mm in major dimension) and, since it occurs with large specimens of *Archegocystis* and *Heliocrinites*, its small size is probably original and not due to preservational selection. *S. pyriformis* may well have been a small species. It is also possible that it may represent the early growth stages of *S. litchi*, a single specimen of which is known from the Rhiwlas Limestone. Pyrite occurs patchily and is a much later diagenetic effect than at Sholeshook. In the Rhiwlas Limestone pyrite occurs as irregular concentrations and cubes which cut across fossil and sediment grains in an irregular manner.

To summarize, *Sphaeronites* found in clastic sediments are not preserved *in situ*, but probably have not been transported very far. The presence or absence of oral and anal cover plates may be an indication as to either how rapidly the individuals were buried after death (i.e. the rate of sedimentation) or of the amount of transport. Both species of *Sphaeronites* *s.s.*, *S. (S.) minor* and *S. (S.) pomum*, rarely have the cover plates preserved and occur in sediments which on other evidence appear to have accumulated very slowly, whereas cover plates are commonly present on all the species of *Peritaphros*. *S. pyriformis* seems to have been more disturbed than other species. In Wales, *Sphaeronites* localities lie towards the edge of the shelf in relatively deep water compared with many Scandinavian localities. Associated cystoids can be divided into two groups. Directly attached forms with exothecal pore structures are usually preserved as complete or partial thecae and probably lived in association with *Sphaeronites*. They were all better adapted to live in water with suspended sediment. The other group are all free-living or attached rhombiferans with stems and endothecal pore structures, which are preserved as isolated plates in most cases. Endothecal pore structures would become clogged in sediment-laden water, which suggests that these cystoids lived further from the sites of deposition and not in association with *Sphaeronites*, an idea confirmed by their fragmentary remains.

PALAEOECOLOGY

Sphaeronites were directly attached by the base of the theca and a more or less definite attachment area can be recognized in most specimens. Nevertheless, exceedingly few specimens are preserved attached to their substrates. The relatively rare instances which do occur invariably involve a *Sphaeronites* epifaunal on another echinoderm, most often another *Sphaeronites*. Despite the rarity of attached specimens, attachment areas are frequently undamaged and we think that *Sphaeronites* attachment may have been effected, in life, by the epidermis rather than by direct cementation of the test to the substrate. Thin sections of *Sphaeronites* epifaunal on other echinoderms show no interpenetration of stereom structure, although the stereom of the epifaunal example may penetrate diplopore canals. On death, decay of the epidermis would allow detachment without damage to the attachment area.

Sphaeronites were filter-feeders and apparently colonized any substrate that was sufficiently stable for them to grow on. Competition for food with other filter-feeding organisms does not seem to have been a serious problem to judge from the rich brachiopod faunas which accompany most *Sphaeronites* species. All *Sphaeronites* were probably low level filter-feeders in life, and show little, if any, evidence of thecal elongation or development of an aboral stem-like projection which would have raised the food-gathering organs off the substrate.

Sphaeronites were apparently gregarious, a mode of life which increases the chances of successful breeding in all sessile benthos. Earlier species (*S. pomum* and *S. minor*) may have been more strongly gregarious than later species and occurred in millions, to judge by the *Sphaeronites* beds in Kinnekulle and on Öland. Later forms (*S. litchi*, *S. variabilis*, etc.) may not have been so strongly

gregarious since they occur in less dense populations associated with a greater variety of other echinoderms. Indeed, an overall change occurs throughout the Ordovician from low diversity and high abundance in the Arenig species to low abundance and high diversity in the Ashgill forms. Thus it seems possible that competition among echinoderms increased significantly as more species became adapted to the same or similar environments.

FUNCTIONAL MORPHOLOGY

Although most palaeontologists agree that fossils should be regarded as once-living things and many accept a Darwinian view of evolution in which competition and selection play important roles, surprisingly few systematic accounts of the vital functions of fossils or functional interpretations of evolutionary trends have been published. In this section we review information about how *Sphaerionites* performed the vital functions necessary for life, such as feeding, breathing, protection, etc. Where data are adequate, we also consider how the performance of these functions changed during growth and evolution. In appropriate cases we erect a paradigm for the function and then compare the actual morphology with this ideal.

Protection

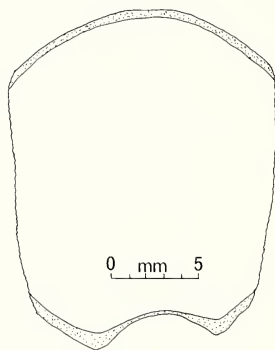
In *Sphaerionites*, as in other cystoids, protection of the soft anatomy was provided by the theca which forms a protective envelope. The paradigm for a protective envelope would be as strong as possible, completely enclose the vital organs, and lack any apertures. However, such a paradigm would isolate the internal organs from the surrounding sea water which contains all the food and oxygen necessary for life, and might pose problems in growth. The paradigm for any one function should contain a qualification that it does not seriously interfere with any other vital function. In *Sphaerionites* the conflicting requirements of protection on the one hand, and of feeding and respiration on the other, are overcome by special ambulacral orifices at the corners of the peristome for the entry of food particles and by the diplopores for respiration. Requirements of protection were met during growth by the theca being composed of tessellated plates, which themselves grew in such a way that no spaces developed between them and which increased in thickness as the theca enlarged. We first compare the construction of the theca in *Sphaerionites* with the paradigm of a protective envelope and then consider the compromises between the conflicting requirements of protection, feeding, respiration, and growth.

As in most other echinoderms, the theca of *Sphaerionites* is composed of individual plates which were an intimate meshwork of calcite, collagen fibres, and soft tissue in life (see Moss and Meehan 1967, for an account of the structure in a living echinoid). As with all organic skeletons, the plates are made of a composite material which, in this case, combines the strength of calcite with the elasticity of collagen and soft tissue, to overcome the brittle nature of the strong component, calcite. A measure of the success of this composite can be seen in the fact that although each plate is a single crystal of calcite, when damaged in life plates do not fracture along calcite cleavage planes. In general, the shape and arrangement of the strong component controls the distribution of strength in a composite material (Wainwright *et al.* 1976, p. 298, principle 4a) so that the strength of a granular composite is largely isotropic while that of fibrous or laminar composites is markedly anisotropic. In all echinoderms the arrangement of the stereom meshwork gives a clue to the distribution of strength within a plate, or the test as a whole. In *Sphaerionites*, as in most cystoids and echinoids where details of the plate structure are known, each plate consists of an inner laminar layer, outer fibrous layer, and the external surface tends to be granular (Paul 1971, 1977). Fibres in the fibrous layer are made of calcite and collagen and lie perpendicular to plate sutures (Paul 1971; Moss and Meehan 1967). The sheets of the laminar layer are parallel to the test surface. Under stress the test is much stronger parallel to the fibres and in the planes of the laminar sheets. There is less chance of the plates dislocating along sutures in life and this type of damage does not normally occur in living echinoderms. Thus, in general, echinoderm plates have less resistance to stresses operating perpendicular to their test surface, but are highly resistant to any stresses which lie parallel to the

plate surfaces. When assembled to form a test like that of *Sphaeronites*, stresses are predominantly transmitted within the plates, not perpendicular to their surfaces. The anisotropy of strength in the plates of *Sphaeronites* is precisely that which would be needed to accommodate stresses induced by wave or current action or the activities of predators.

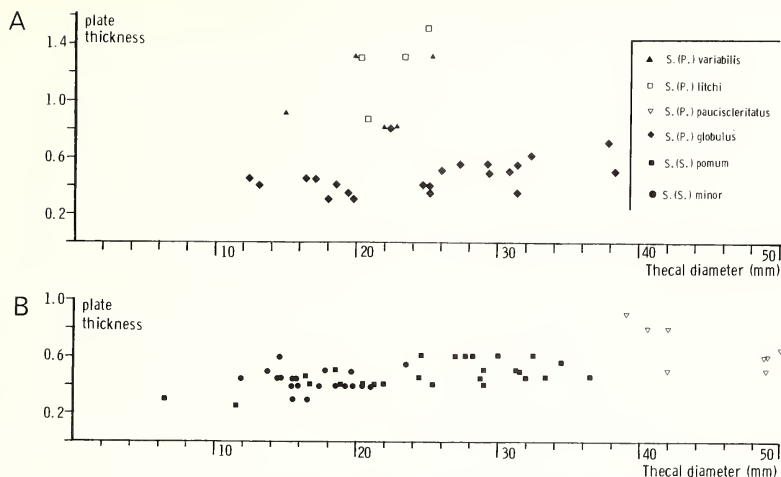
The theca of *Sphaeronites* is frequently spherical, an ideal shape which encloses the maximum volume with the minimum constructional material. Juveniles and other examples with relatively large attachment areas may depart from the ideal sphere and have cylindrical or fusiform thecae. The theca is composed of randomly arranged plates, the thickness of which is fairly constant for a given species. Plates are thickened around the edge of the attachment area and at the oral pole where they form a raised oral platform surrounding the peristome and periproct. In some specimens of *S. (S.) minor* and *S. (S.) pomum* plates forming the attachment area itself are less than half the normal thickness, but presumably the hard substrate provided adequate protection in life. When detached from the substrate these species at least would have been relatively vulnerable. In a theca of uniform thickness and homogeneous construction, strength is inversely proportional to the radius of curvature. In a non-spherical theca where the radius of curvature is smallest one would expect the theca to be thickest if strength is to be maintained. In *Sphaeronites*, and many other directly attached cystoids, the thickest plating occurs at the sharp angle between the attachment area and the sides of the theca as predicted by strength requirements (text-fig. 9). Not only is the theca not of uniform thickness but it is

TEXT-FIG. 9. Camera lucida drawing of the thickness of the thecal wall in *Sphaeronites* (*Sphaeronites*) *minor* sp. nov. to show thin wall over the attachment surface (below) and maximum thickness at the angle between the attachment surface and the lateral wall. Thecal wall stippled. Note pressure solution of test.



not of homogeneous construction either. Moss and Meehan (1967) have shown that, contrary to popular opinion, the plate sutures are not lines of weakness in a living echinoid and this was probably true of *Sphaeronites* as well.

Thecal plates vary in thickness from about 0.25 mm up to 2.5 mm, fit together without any gaps except for the special orifices necessary for feeding, etc., and lack weak spots. They completely enclose the vital organs and compare well with the paradigm of a protective envelope. During growth, plates were added in most species of *Sphaeronites*. Secondary plates start as small triangular plates at the triple junctions of primary plate sutures. In *S. (S.) pomum* and *S. (P.) globulus*, for which the best data were available (text-fig. 10), plate thickness increases slightly with growth. The ratio of plate thickness to maximum plate diameter and of plate thickness to maximum thecal diameter are measures of the strength of plates and thecae, respectively. Table 1 records maximum plate thickness, diameter of plates, and maximum thecal diameter for various species of *Sphaeronites*. A progression in both plate thickness and size occurs from earlier to later species, but the ratio of these remains fairly



TEXT-FIG. 10. A, B. Graphs showing the relationship between plate thickness and mean thecal diameter in *Sphaeronites* s.s. and *Peritaphros* Paul.

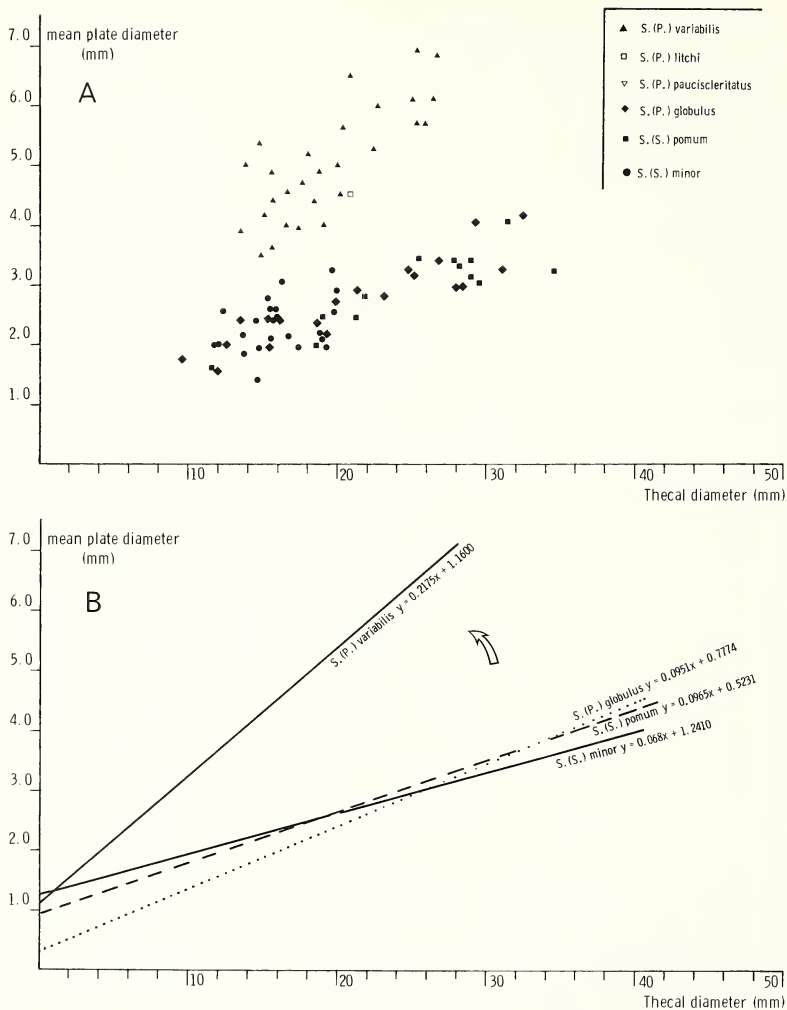
TABLE 1. Maximum measurements of plates and thecae in *Sphaeronites*

Species	Age	Maximum measurement (mm)		
		*Plate thickness	Plate diameter	Thecal diameter
<i>S. minor</i>	U. Arenig	0.6	3.24	23.1
<i>S. pomum</i>	U. Arenig	0.6	4.06	36.5
<i>S. globulus</i>	U. Llandeilo	0.8	4.17	37.9
<i>S. pauciscleritatus</i>	Caradoc	1.0		50.0
<i>S. variabilis</i>	U. Caradoc-	1.3	7.83	26.5
	L. Ashgill			
<i>S. litchi</i>	L.-M. Ashgill	1.5	7.4	39.1

* Measured near the middle of the sides of the theca and therefore not including the thickest parts at the edges of the attachment areas.

constant. The ratio of plate thickness to thecal diameter increases with time and the later species would seem to have had stronger thecae than early species.

The peristome and periproct are relatively large orifices but were protected by cover plates in life. Food entered the peristome through five small ambulacral orifices (text-fig. 13) at the corners of the peristome. There is no evidence that the palatal plates (oral cover plates) were able to open in life. The periproct was covered by an anal pyramid which could open outwards but not inwards, and acted as a one-way valve allowing egress but not entry. It was presumably closed most of the time. Cover plates (palatals and anals) effectively complete the protection afforded by the theca.



TEXT-FIG. 11. Graphs showing the relationship between mean plate diameter and mean thecal diameter. A, scatter diagram; B, best fit lines (arrow indicates evolutionary trend).

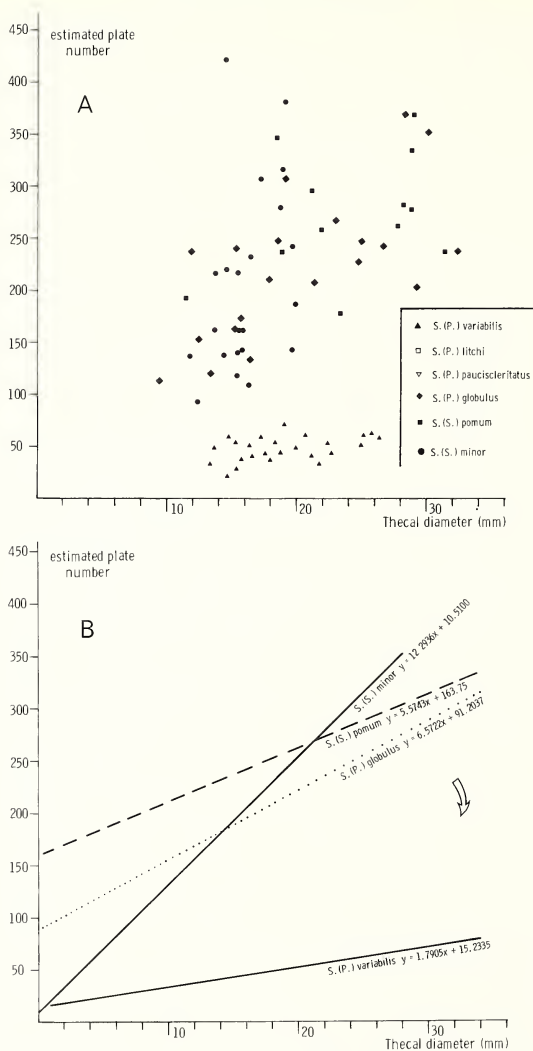
The diplopores were the main respiratory organs (see below) and were covered in life by soft tissue. They were not protected themselves by spines as are the tube feet of modern echinoids, and were presumably subject to predation. We do not think that they were extensible. The soft tissue cover may have been partly protected by the peripheral tubercles of *S. (S.) minor* and *S. (S.) pomum*, but later species lack these features.

Average plate diameter has been estimated by measuring two diameters in up to twenty plates per theca in each species. From these figures we have calculated an estimated plate number per theca (a parameter which is hardly ever directly measurable) by calculating the mean area of thecal plates and the estimated area of the entire theca. Both average plate diameter and estimated plate number increase with growth in all species for which quantitative information is available (text-figs. 11 and 12) as one would expect. However, the rates of increase change during evolution. Low and middle Ordovician species have a relatively high rate of increase in plate numbers, but a low rate of increase in plate size. *S. (P.) variabilis*, the only upper Ordovician species with reasonable data, has a low rate of increase in plate numbers, but a rapid increase in the size of plates. This, coupled with qualitative observations in *S. (P.) pauciscleritatus* and *S. (P.) litchi*, implies that the introduction of new plates played a more important role in thecal growth of low and middle Ordovician species, whereas growth of existing plates was more important in later species. The pattern of thecal growth seems to have simplified during evolution.

Feeding

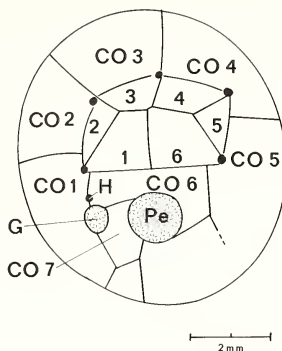
Sphaeronites was a directly attached cystoid. It must, therefore, have been a filter-feeder which trapped food particles using its ambulacral appendages. The latter are never preserved and so their efficiency cannot be compared with any paradigm. Indirect evidence (outlined below) suggests that the appendages were simple unbranched structures with a length approximately equal to thecal diameter. Except in rare examples of *S. (P.) variabilis* with four, five ambulacra occur in all specimens of *Sphaeronites*. Each ambulacrum had one to three facets directly adjacent to the mouth on the border of the oral platform (text-fig. 13). Feeding and respiration rates are closely linked. All species of *Sphaeronites* had approximately the same respiration rates for any given size (text-fig. 20). Changes in respiration during growth were presumably matched by an increase in the length of the ambulacral appendages or by the addition of new appendages. However, as ambulacral facets are only rarely preserved, very little is known about the latter. Thus no direct evidence of changes in feeding during ontogeny or evolution have been recognized.

Something about the nature of the food, assimilation rates, and changes in feeding during growth and evolution can be inferred from the morphology of the oral area. Food particles entered the theca through minute ambulacral orifices at the corners of the peristome and continued to the edge of the mouth along narrow food grooves beneath the palatal plates. The diameters of the ambulacral orifices and food grooves put a maximum limit of about 0.1 mm diameter on food particle size. Particles larger than this would not have been able to enter the theca. The anus, on the other hand, is a relatively large opening of less than 1 mm diameter only in the smallest examples and may reach as much as 3 mm mean diameter in *S. (P.) litchi*. It seems reasonable to infer that the assimilation rate was relatively low and the faeces bulky in *Sphaeronites*. In other words, a large proportion of the food trapped by the ambulacral appendages was not digested completely, the particles were packed together in the gut, and voided as relatively bulky pellets, up to twenty or thirty times the diameter of the ingested food particles, possibly even more. Such an arrangement would adequately prevent any fouling of the food-gathering apparatus and explains the consistently close association of the mouth and anus in the superfamily Sphaeronitida. On this assumption, the size of the anus may reflect the volume of material collected by the food-gathering organs and passed through the gut. Text-fig. 14 shows that during growth and evolution changes in the size of the anus occurred. The rate of ontogenetic size increase is lowest in the early species, *S. (S.) minor*, and highest for the youngest species for which adequate data exist, *S. (P.) variabilis*. Since there appears to be relatively little change in respiration rate between these species, the apparent increase in food-processing capacity may reflect more rapid growth in later species.



TEXT-FIG. 12. Graphs showing the relationship between estimated plate number and mean thecal diameter. A, scatter diagram; B, best fit lines (arrow indicates evolutionary trend).

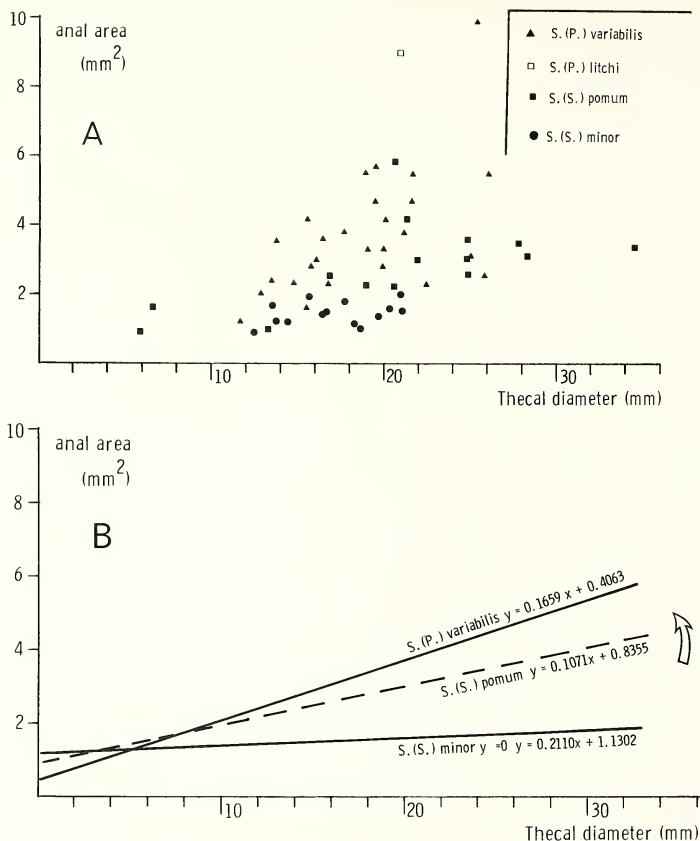
TEXT-FIG. 13. Diagrammatic oral area of *Sphaeronites* (based on *S. (Peritaphros) variabilis* sp. nov. RM Ec25419). 1-6, oral cover plates (palatals); CO1-CO7, circumoral plates; G, gonopore; H, hydropore; Pe, peripore.



Respiration

Physiologists insist that respiration is an internal chemical process and that the process in our lungs, for example, is merely gas exchange. Only the latter can be considered here. The diplopores were the most important sites of gas exchange in *Sphaeronites*. Although the surface tissue and ambulacral appendages were bathed directly in sea water, all the internal organs received oxygen via the diplopores. In each diplopore two perpendicular canals pass right through the test and open externally in a pit or trough called the peripore, which was covered with soft tissue in life. Oxygen diffused in, and carbon dioxide out, through the soft tissue cover. In *Sphaeronites s.s.* the peripore is sunken, usually oval, and surrounded by a raised rim which bears tubercles or blunt spines (text-fig. 5A; Pl. 73, fig. 6). In *Peritaphros*, the two perpendicular canals open externally on either side of a large central tubercle and the peripore is reduced to a moat-like channel around the central tubercle (Pl. 73, fig. 7). The rim around the peripores is usually polygonal in outline and never bears tubercles or blunt spines. The new subgenus, *Ataphros*, is erected here for a species of *Sphaeronites* with diplopores in which only the central tubercle and perpendicular canals remain (Pl. 73, fig. 8). All trace of the peripore is lost, hence the subgeneric name, *Ataphros* (Greek, without a canal). In all three types of diplopores the same general circulation existed, with coelomic fluids ascending one perpendicular canal, gaining oxygen, and losing carbon dioxide via the soft tissue cover and the oxygenated fluids descending back into the thecal cavity via the other perpendicular canal. Separation of oxygenated and deoxygenated water was thus maintained within the diplopores.

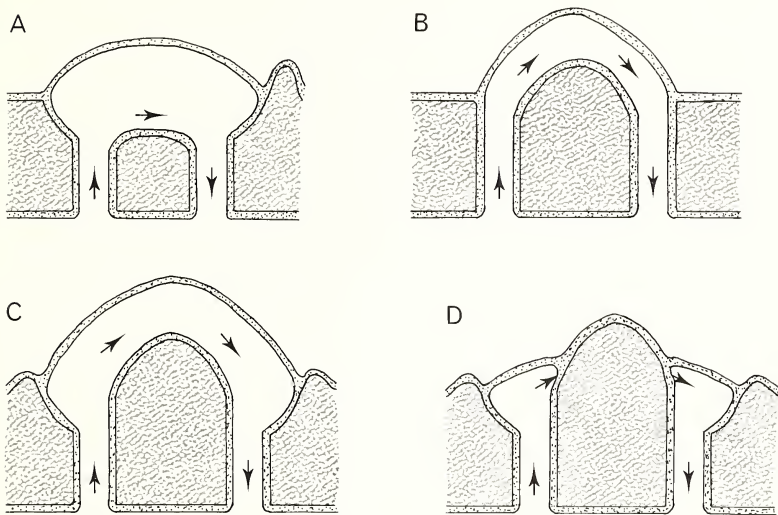
In diplopores of *Sphaeronites s.s.* we have assumed a flat soft tissue cover over the entire area of the peripore (text-fig. 15A). In life the actual cover may have extended away from the thecal surface to some (unknown) extent which would have increased the potential exchange surface, but may not have achieved more efficient exchange (see below). In the diplopores of *Peritaphros* the soft tissue cover can be restored in two different arrangements (text-figs. 15C, D). It may either have continued over the central tubercle as in *Sphaeronites s.s.* or it may have been confined to the moat-like channel around the central tubercle. Computer-generated estimates of the exchange capacity of either arrangement show that in the former, exchange rates of *Peritaphros* were about the same or slightly greater than those for *Sphaeronites s.s.*, while the latter arrangement gave values about one-tenth those of *Sphaeronites*. We have concluded therefore that the former arrangement was the more likely. Other features of morphology suggest that the two subgenera had similar growth rates and food-gathering capacities and it seems likely that they also had similar respiratory capacities. In *Ataphros* we also assume that the soft tissue cover continued over the central tubercle (text-fig. 15B), but estimates of exchange capacity are impossible as we cannot measure the other parameters of the



TEXT-FIG. 14. Graphs showing the relationship between area of periproct and mean thecal diameter. A, scatter diagram; B, best fit lines (arrow indicates evolutionary trend).

diplopores. We believe that the change from *Sphaeronites s.s.* to *Peritaphros* involved an increase in the efficiency of the circulating currents. In the diplopores of *Sphaeronites* coelomic fluids may take a short cut between the perpendicular canals without coming into intimate contact with the exchange surface (text-fig. 15A). In the diplopores of *Peritaphros*, however, the large central tubercle ensures that the fluids come close to the soft tissue cover. In our reconstructions we have assumed a gap between the central tubercle and the soft tissue cover equal to the perpendicular canal diameter. The change ensured a greater ratio of exchange surface area to peripore volume in the diplopores of

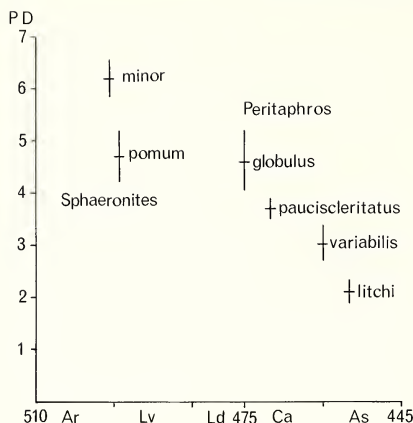
Peritaphros, and the elimination of the peripore walls in *Ataphros* may have taken this a stage further. Stratigraphically, *Sphaeronites* s.s. is confined to the upper Arenig or lowest Llanvirn of Sweden; *Peritaphros* ranges from the Llandeilo to the middle Ashgill, while *Ataphros* is only known from the lower Ashgill of South Wales. The stratigraphic occurrence of the three types of diplopores suggests evolution towards more efficient types of diplopores on the interpretations made in text-fig. 15.



TEXT-FIG. 15. Inferred soft tissue cover in diplopores of *Sphaeronites* s.s. (A), *Ataphros* subgen. nov. (B), and two alternatives for *Peritaphros* Paul (C and D). Computer programs infer that reconstruction (C) is more likely. Soft tissue stippled. Arrows indicate current direction for internal coelomic fluids.

In addition to this change in overall morphology, the density of diplopores on the thecal surfaces decreases throughout the Ordovician (text-fig. 16; see also Paul 1973, fig. 14b), from a high of over six diplopores per mm² in *S. (S.) minor* sp. nov. to a low of about one and half per mm² in *S. (P.)* sp. A. The original measurements of diplopore density (Paul 1973) were made on a limited sample using a squared graticule eyepiece in a binocular microscope. Some additional measurements used in this paper were made by Bockelie from camera lucida drawings. Despite the different techniques and sample sizes, both the actual density measurements and the overall trends found were very similar so we have combined our data in this paper.

Diplopore density is effectively independent of size (text-fig. 18) over a range of thecal diameters from 9 to 38 mm in *S. (P.) globulus* and from 11 to 26 mm in *S. (P.) variabilis*. The decrease in the density of diplopores through the Ordovician is at least partly due to an increase in their size as well as a change in the closeness of packing. To investigate and interpret this trend more thoroughly we made the measurements shown in text-figs. 7D and 7E. We find (Table 2) that the diameter and separation of the perpendicular canals do not change greatly, but that the width of the peripores shows a marked increase throughout the Ordovician. Computer programs indicate that it is more efficient to increase



TEXT-FIG. 16. Evolutionary trend towards declining diplopore density in *Sphaeronites* throughout the Ordovician. Horizontal lines represent mean pore-density, vertical bar $\pm$ one standard deviation. PD, pore density. Horizontal scale in millions of years and series. Ar, Arenig; Lv, Llanvirn; Ld, Llandeilo; Ca, Caradoc; As, Ashgill. In all cases the age of each species is taken as that of its *first* occurrence.

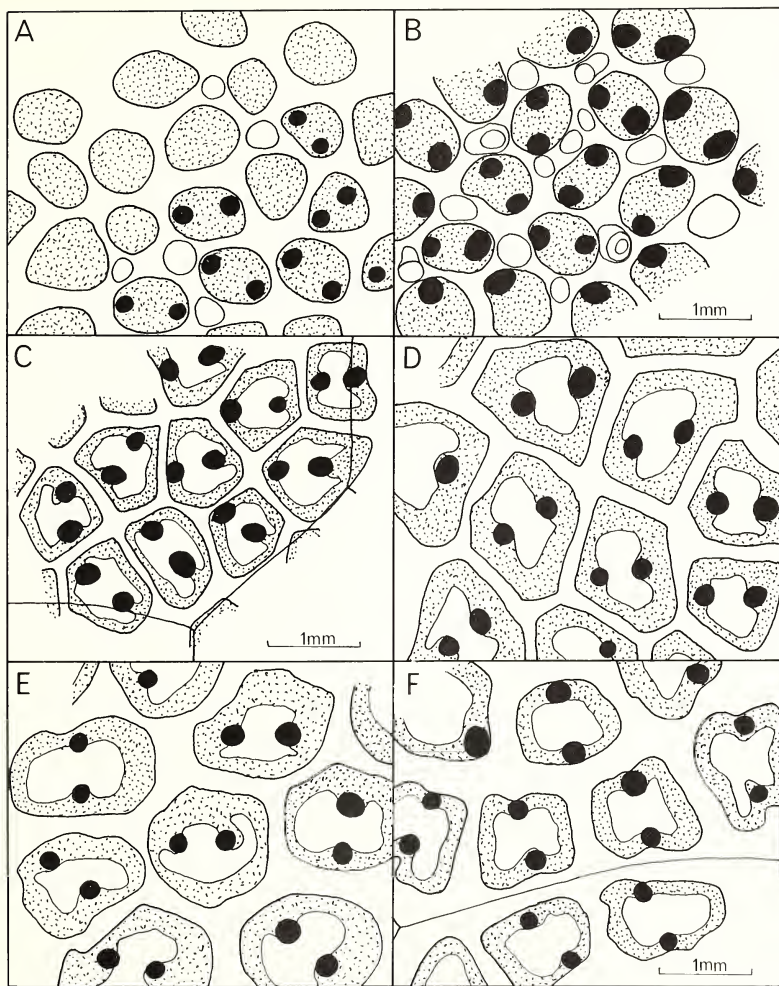
the area of the exchange surface by widening it perpendicular to the current direction than by lengthening it parallel to the current direction (Paul 1978, p. 282). Thus the trend appears to reflect a means of increasing the efficiency of the diplopores by enlarging their width in preference to their length. In *S. (P.) litchi* a further modification occurred because the central tubercle rises well above the general test surface. Thus, although the separation of the perpendicular canals is almost the same as that of the much older *S. (S.) pomum*, the actual path followed by the coelomic fluids was considerably longer, probably further than in *S. (P.) variabilis* which has the widest separation of perpendicular canals of any species.

One of us has developed computer programs to simulate the gas exchange in the diplopores, the main details of which have been published elsewhere (Paul 1978). These programs were used to investigate quantitatively the functional significance of the changes in the diplopores of *Sphaeronites*. Before presenting the results, a brief review of the assumptions of the computer programs and reconstructions of the mode of functioning of *Sphaeronites* diplopores is necessary.

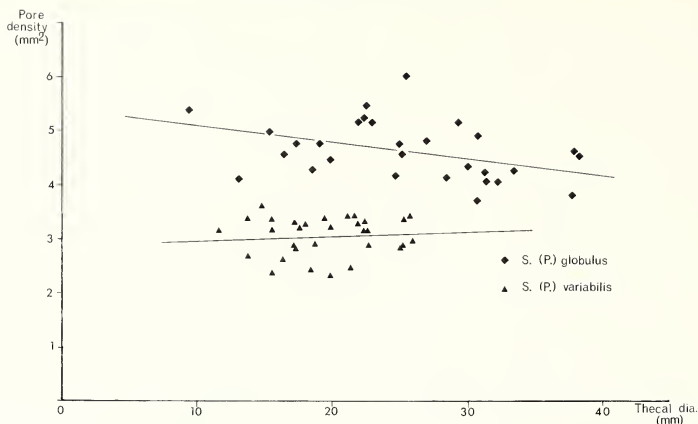
TABLE 2. Mean measurements of diplopores in *Sphaeronites*

Species	Mean Measurements (mm)					
	Perpendicular canal separation	*N	Perpendicular canal diameter	*N	Peripore width	*N
<i>S. minor</i>	0.2437	24	0.0674	24	0.2404	24
<i>S. pomum</i>	0.2914	30	0.0709	30	0.2802	29
<i>S. globulus</i>	0.2383	20	0.0936	20	0.3983	17
<i>S. pauciscleritatus</i>	0.2667	9	0.0506	9	0.3866	9
<i>S. variabilis</i>	0.3447	28	0.0693	20	0.4374	28
<i>S. litchi</i>	0.2889	7	0.0998	7	0.6169	7

* N is the number of specimens on which measurements were made. Up to twenty measurements were made of perpendicular canal separation, up to forty for perpendicular canal diameter, and up to sixty for peripore width, on each specimen.



TEXT-FIG. 17. Camera lucida drawings of the diplopores of species of *Sphaeronites* s.s. and *Peritaphros* Paul. A, *S. (S.) minor* sp. nov.; B, *S. (S.) pomum*; C, *S. (P.) globulus*; D, *S. (P.) variabilis* sp. nov.; E, *S. (P.) pyriformis*; F, *S. (P.) litchi*. Perpendicular canals black; peripores stippled; peripore walls and tubercles white.

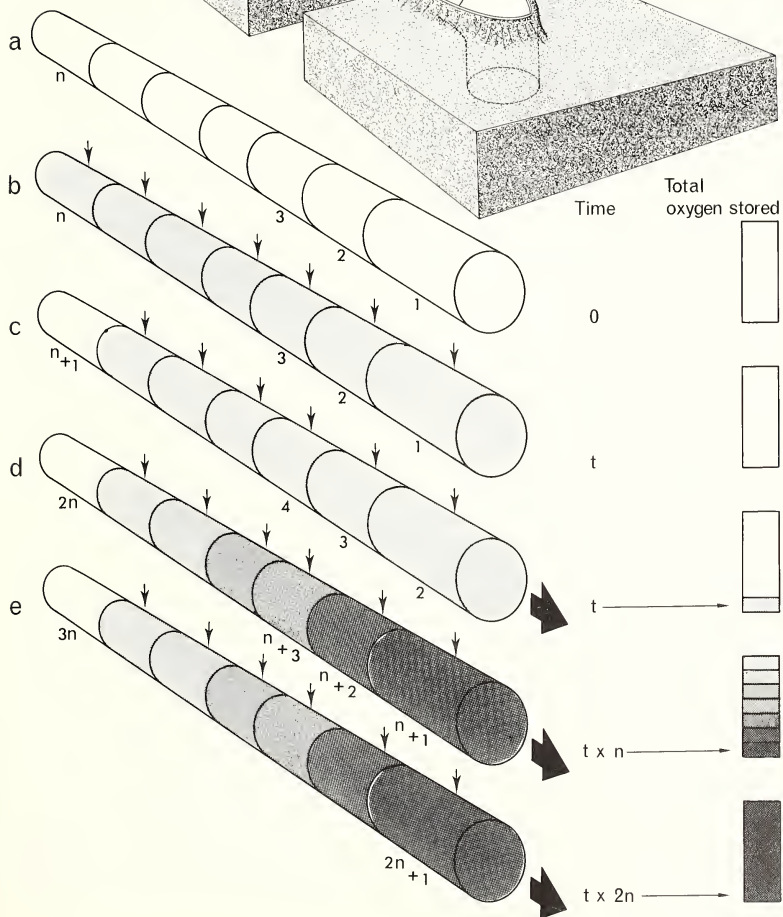
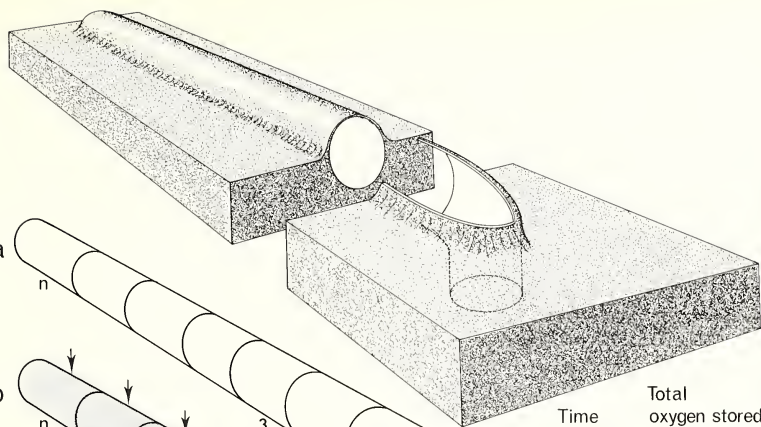


TEXT-FIG. 18. Graph showing the relationship between diplopore density and mean thecal diameter. Solid lines represent Bartlett's best fit lines.

Oxygen exchange in the diplopores of Sphaerionites. Carbon dioxide diffuses more rapidly than oxygen through all types of living tissue. Hence it is diffusion of oxygen which limits rates of gas exchange and we have only considered transport of this gas. Oxygen (and any other gas) will diffuse across a permeable membrane from high to low concentrations at a rate controlled by the following factors: the thickness, area, and permeability of the membrane, the difference in concentrations (partial pressures) on either side of the membrane, and the temperature. Krogh (1919, p. 408) listed the diffusion constants of oxygen through various substances and we have used his value for connective tissue—namely, 0.115 ccs per μm thickness, per cm^2 area, per minute @ 20°C and one atmosphere pressure difference.

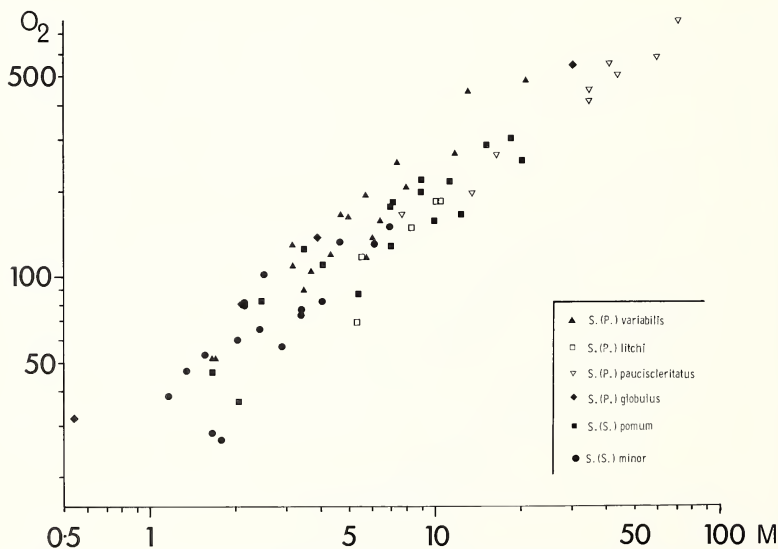
Assumptions of the computer programs. The computer program divides a canal (in this case a diplopore) into narrow slices (0.01 mm thick) perpendicular to the length (i.e. the current direction) and calculates the amount of oxygen that will diffuse into each strip in turn for a brief period which is determined by the current velocity (text-fig. 19). It then moves each strip along one place to simulate current flow and recalculates the amount of diffusion, keeping a running total of the amount of oxygen transferred. The length of a diplopore has been calculated by measuring the separation of the perpendicular canals (measurement 13, text-fig. 7b) for twenty diplopores on each specimen and taking the average. Diplopore length in the computer programs is slightly less than the real path followed by coelomic fluids in life, and hence exchange will be marginally low. However, the error should be consistent for all specimens. Diplopore width has been taken as the average of the three

TEXT-FIG. 19 (*opposite*). Diagram to illustrate the basis of the computer programs. *a*, starting time (0) with canal divided into empty cells; *b*, canal with some oxygen in it after diffusion (small arrows) for time t ; *c*, cells shifted to simulate current flow (large arrow) and contents of cell 1 stored; *d*, after first cycle (time nt) with contents of n cells stored; *e*, situation after a second cycle (time $2nt$) with store full of cells with maximum oxygen concentration. The store is set to zero after each cycle. Rate of exchange is the total oxygen in the store divided by the time.



widths measured (measurements 14–16) in text-fig. 7D, again taken from twenty diplopores per specimen. As with length a slight inaccuracy must occur, but it should be consistent for all specimens. Mean thecal diameter (of an equivalent sphere) and diplopore density are also fed into the program which then calculates the rate of oxygen transfer for an average diplopore. Total thecal-surface area divided by the diplopore density gives an estimated total number of diplopores and hence total exchange per whole animal. We assume that all this oxygen was used by the internal organs only. The surface epithelium was bathed in sea water and oxygenated directly in life. Thus in comparing calculated exchange rates with published rates for living echinoderms, some allowance must be made for the proportion of internal respiration compared with epithelial respiration. Published estimates vary from 10 to 60% (Webster and Giese 1975; Farmanfarmaian 1966). We have chosen 50%, and the figures quoted for total exchange rate in this paper are exactly twice those calculated by the computer programs for transfer through the diplopores. Again this may be inaccurate, but it is consistent for all specimens of all species and hence evolutionary and growth comparisons are valid. In living animals respiratory rate varies with size, among other things. So the programs calculate the mass of each specimen in life assuming that soft tissue had a specific gravity of one and that the test was 50% calcite and 50% soft tissue. Exchange rates are quoted as qO_2 in μl per hour per whole animal. These are plotted on a log:log graph (text-fig. 20). The slopes of any best fit lines indicate how qO_2 in ml per hour per g changes with growth.

Reconstruction of the mode of functioning of Sphaeronites diplopores. We assume that body fluids passed up one perpendicular canal, travelled along the peripore which was roofed with soft tissue,



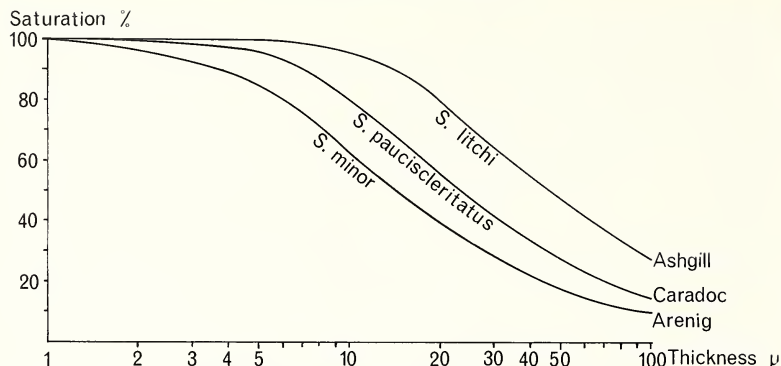
TEXT-FIG. 20. Graph of whole echinoderm exchange rates for species of *Sphaeronites s.s.* and *Peritaphros* Paul. Note that there is very little change between species. M, thecal mass in g; O_2 , μl per hour per whole animal.

and returned down the other perpendicular canal. Specialized respiratory tube-feet of modern echinoids have ciliated external epithelium, but the internal epithelium is only ciliated where it passes through the test (Nichols 1959b, p. 539). Hence we have accepted Gray's (1928, table 5, p. 76) velocity of 0.06 cm per second for ciliary currents at 20 °C as the velocity of the coelomic fluids within the perpendicular canals. Elsewhere in the peripore the current velocity will have been inversely proportional to the cross-sectional area at any point. We have assumed a flat cover to the peripore in *Sphaeronites* s.s. and calculated current velocity accordingly. In *Peritaphros* we have assumed that the cover was continuous and raised over the central tubercle by the width of the tangential canals (measurement 19, text-fig. 7E). Again current velocity within the peripore has been calculated accordingly.

We have assumed that the surrounding sea water was saturated with oxygen at present day levels (0.0052 ml per litre at 20 °C), which incidentally also assumes present day salinity levels. We are aware that Ordovician oceans may not have contained the same amounts of salts or gases. However, the assumption is the only one reasonable if the results are to be compared with known exchange rates in living echinoderms, since most respirometry experiments involve saturated sea water. Oxygen diffuses approximately three times as fast through sea water as through connective tissue (Krogh 1919, p. 408), and since the diplopores were, so to speak, bathed in an infinite reservoir of oxygenated sea water, we have assumed that all oxygen removed from sea water adjacent to a diplopore was replaced immediately. Nichols (1959a, p. 84; 1959b, p. 551) gives thicknesses of 1–3 and 10 μm respectively for the walls of respiratory tube-feet in *Echinocyamus pusillus* (O. F. Müller) and *Echinocardium cordatum* (Pennant). To judge from his figures, Fenner (1973) gives values ranging from about 10 to 105 μm for other modern echinoids, while Smith (1978) gives values of 2–10 μm for specialized respiratory tube-feet of regular echinoids. Hence we have run the *Sphaeronites* programs with assumed thicknesses from 5 to 100 μm for the walls of *Sphaeronites* diplopores. There are reasons, outlined below, for believing that the actual thickness was between 10 and 50 μm and a standard thickness of 20 μm has been used in evolutionary comparisons. Results (text-fig. 20) are presented as a log:log plot of exchange rate against thecal mass.

Results

Text-fig. 20 shows no clear evolutionary trend in respiratory capacity, although there is an obvious increase in total gas exchange with growth. Exchange rates for living animals are frequently quoted in μl per g, and this value decreases with increased size during ontogeny in *Sphaeronites* as in all other invertebrates. From text-fig. 20 it would seem that the evolutionary trend in diplopore density, together with the changes in diplopore morphology, had very little effect on the total respiratory exchange. However, if the degree of saturation with oxygen achieved within the diplopores is compared, a distinct trend appears. Text-fig. 21 shows per cent saturation plotted against thickness of cover for three species, *S. (S.) minor*, *S. (P.) globulus*, and *S. (P.) litchi*. The other species fit on the graphs in accordance with their stratigraphical position, but make the diagram less clear so they have not been plotted. Thus it would seem that the evolutionary trend in diplopore density achieved approximately the same exchange rate, but with progressively fewer, more efficient diplopores. This evolutionary increase in saturation can be used to estimate the thickness of the soft tissue cover to the diplopores if one assumes that the trend arose through natural selection. Selection could only have been effective at thicknesses which produced a considerable change in saturation. For example, with an infinitely thin membrane, diplopores of all species of *Sphaeronites* would have achieved 100% saturation. Equally, with an infinitely thick membrane, 0% saturation would occur in all species. Text-fig. 21 shows that the maximum change in saturation occurs at about 20 μm thickness, from about 39% in *S. (S.) minor* to about 79% in *S. (P.) litchi*. This thickness is somewhat greater than occurs in respiratory tube-feet of modern sea urchins (Andrew Smith, pers. comm.), but it is not by any means impossible. Of course, the possibility that different species of *Sphaeronites* may have had diplopore walls of different thickness cannot be excluded, but we have no means of determining this at present. A standard thickness of 20 μm has



TEXT-FIG. 21. Graph showing the relationship between saturation of coelomic fluids and thickness of peripore cover in one early, one middle, and one late Ordovician species. Maximum difference in saturation, on which selection could have operated, is at 20μ . This thickness was adopted as standard in all other computer programs.

been assumed in comparisons between species because this thickness produces the maximum change in saturation.

If we accept the 20μ thickness for the diplopore walls, it becomes possible to convert the maximum exchange rate into calorific and food values. One litre of oxygen used in metabolism yields approximately 4.8 kcal. Various foodstuffs also yield known ranges of calories on oxidation (Prosser *et al.* 1950, table 40, p. 237) as follows:

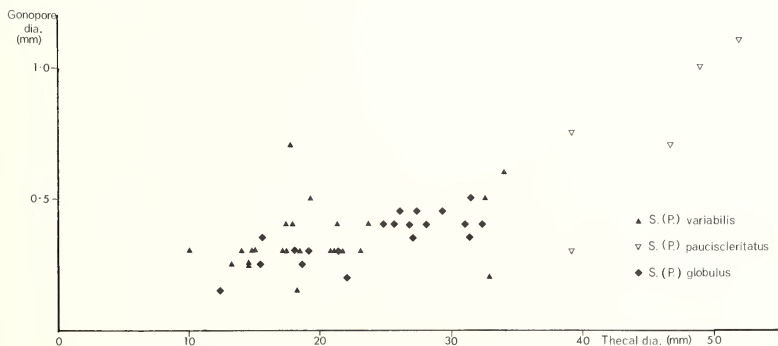
1 g carbohydrate yields	4.2 kcal
1 g protein yields	4.2 kcal
1 g fat yields	9.5 kcal

Available data on the food of modern crinoids are very meagre (Rutman and Fishelson 1969), but suggest that it was composed mainly of protein and carbohydrate, rather than fat. Taking an average figure of 4.2 kcal per g, this gives an oxygen equivalent of 1.143 g of food per litre of oxygen. *Sphaerionites* species had potential exchange rates which varied from twenty-eight to 623μ oxygen per hour, which convert to a maximum food consumption of 32.004 to 712.089μ food per hour. Present-day sea water contains wide ranges of suspended organic matter, but a range of 1.5 mg ($1000\text{--}5000 \mu$ g) per litre is reasonable for shallow seas such as *Sphaerionites* inhabited. Taking the lower figure, this gives filtration rates of 32–712 ml per hour. These figures may be used to estimate the length of the food-gathering organs in *Sphaerionites*, which are never preserved and remain largely unknown in the Diploporita generally. Brachioles in rhombiferans are generally 0.5 mm in diameter, and if we assume tube-feet 250μ m long stretched widely on either side then each brachiole could filter a path 1 mm wide. With a ciliary current of 0.06 cm per second the required volumes of water represent filter areas from 14.8 to 330 mm^2 in thecae ranging from 5 to 50 mm diameter. If the appendages were all of equal length and if half the food ingested was assimilated, this gives a minimum of five brachioles (i.e. one per radius) about 6 mm long in a 5 mm diameter theca and a maximum of fifteen brachioles (i.e. three per radius) about 44 mm long in a 50 mm diameter theca. Thus throughout the growth of all *Sphaerionites* species, unbranched appendages of a length approximately equal to the thecal diameter could have gathered sufficient food to utilize all the oxygen absorbed by the animals.

REPRODUCTION

Although hermaphroditism is known among living echinoderms, most species have separate sexes. We assume this was the case in *Sphaeronites*, but there is no evidence of sexual dimorphism to confirm it. Each specimen has a single gonopore and hence had a single internal gonad in life. The diameter of the gonopore increases slowly with increasing thecal size (text-fig. 22) and there is no clear evolutionary trend affecting the position or size of this orifice. Presumably eggs and sperm were shed directly into the sea water. Modern starfish and echinoids have a trigger, the shedding substance, which induces simultaneous shedding among mature adults of the same species. Such a mechanism is most effective if all individuals shed for approximately the same time-span. The increase in the diameter of the gonopore during growth may be interpreted as a mechanism to speed up shedding from a (presumably) larger internal gonad. The scatter of gonopore diameters in *S. (P.) globulus* (text-fig. 22) suggests a relatively rapid increase at about 22–24 mm thecal diameter. This might indicate the onset of sexual maturity, but equally it may simply arise by chance. More observations are required before this idea can be confirmed.

The previous consideration of the vital functions of *Sphaeronites* throughout growth and evolution suggests that later species were better protected than earlier ones, and that their diplopores achieved the same exchange capacities in a more efficient manner. Although our calculations make a large number of assumptions, we are convinced that they contribute to an understanding of the mode of life and evolution of *Sphaeronites*. In particular, quantitative analysis of feeding and respiration using computer programs has allowed us to reconstruct with some confidence anatomical features in *Sphaeronites* which have never been found preserved and hence cannot be observed directly. We can suggest that the cover to the diplopores in *Peritaphros* was continuous over the central tubercle, rather than confined to the moat-like channels of the peripore because the latter arrangement gives only a tenth the exchange capacity. We can suggest that the cover of all diplopores in *Sphaeronites* was 20 μm thick, because then selection would have been most effective in increasing saturation of coelomic fluids. Finally, we can suggest that the food-gathering organs were probably unbranched and about as long as the thecal diameter because they could then gather adequate food to utilize the maximum amount of oxygen the animals could absorb. In our view such quantitative studies are a powerful tool in functional interpretations of extinct organisms.



TEXT-FIG. 22. Graph showing the relationship between gonopore diameter and mean thecal diameter in *Sphaeronites* s.s. and *Peritaphros* Paul.

SYSTEMATIC PALAEONTOLOGY

Class DIPLOPORITA Müller, 1854

Superfamily SPHAERONITIDA Neumayr, 1889

For definition see Paul (1973, p. 18). The Superfamily Sphaeronitida contains two families, the Sphaeronitidae and the Holocystitidae. They are distinguished on their pore structures (diplopores *s.s.* in the Sphaeronitidae, humatipores in the Holocystitidae), on details of the plating arrangement in the oral area, and on ambulacral structures. For details see Paul 1971, pp. 68–72 (holocystitids), 1973, pp. 18, 19 (sphaeronitids).

Family SPHAERONITIDAE Neumayr, 1889

Diagnosis. 'A family of Sphaeronitida with diplopores; peristome surrounded by six circum-oral plates with a small additional plate (CO7) between the peristome and periproct, but not in contact with the former; four or five ambulacra with one or more ambulacral facets each. (Paul 1973, pp. 18, 19).

Genus *Sphaeronites* Hisinger, 1828

- 1772 *Echinus* Gyllenhaal (*pars, non* Linnaeus, 1758), p. 242.
- 1818 *Echinospaerites* Wahlenberg (*pars*), p. 54.
- 1828 *Sphaeronites* Hisinger, p. 195.
- 1854 *Sphaeronites* Hisinger; Müller, p. 186.
- 1878 *Sphaeronis* [*sic*] Hisinger; Angelin, p. 30.
- 1879 *Sphaeronites* Hisinger; Zittel, p. 417.
- 1896 *Pomonites* Haeckel, p. 96, fig. 6.
- 1896 *Sphaeronites* Hisinger; Haeckel, p. 98, fig. 7.
- 1899 *Sphaeronites* Hisinger; Jaekel, p. 396.
- 1900 *Sphaeronis* [*sic*] Hisinger; Bather, p. 71.
- 1943 *Sphaeronites* Hisinger; Bassler and Moodey, pp. 6, 189.
- 1945 *Sphaeronites* Hisinger; Regnéll, p. 161.
- 1967 *Sphaeronites* Hisinger; Kesling, p. S243, fig. 142: 1a–e.
- 1973 *Sphaeronites* Hisinger; Paul, p. 19.

Type species. *Echinus pomum* Gyllenhaal, 1772, by original designation, Müller 1854, p. 242, pl. 8, figs. 1–3; from the Asaphus Limestone (Arenig), Kinnekulle, Västergötland, Sweden.

Diagnosis. A genus of Sphaeronitidae with globular to pyriform or fusiform theca composed of forty to two hundred or more plates which are irregularly arranged except in the oral area; peristome and periproct very close together on smooth oral prominence; five ambulacra with one to three facets each; all thecal plates uniformly covered with randomly orientated diplopores (except in attachment area); attachment direct.

Remarks. The most characteristic features of the genus are the very close approximation of the peristome and periproct, both of which are developed in a smooth, diplopore free area at the oral pole; and the evenly and densely developed diplopores. Other sphaeronitid genera (e.g. *Eucystis*, *Archegocystis*, *Diplosphaeronis*) have the anus much further from the mouth, while the diplopores of *Haplosphaeronis* and *Palaeosphaeronites*, two genera with closely approximated peristomes and periprocts, are quite different from those of *Sphaeronites* as here understood. All genera except *Diplosphaeronis* have much more widely spaced diplopores which usually have oval peripores.

Close examination of the diplopores of *Sphaeronites* has shown that they fall into three distinct types. In the type species, *S. pomum* (Gyllenhaal), all the diplopores are deeply sunken into the thecal surface, have oval or rounded peripores, and have small blunt spines developed on the peripore rim (Pl. 73, fig. 6; text-fig. 5A). In contrast, the diplopores of *S. globulus* (Angelin) are not deeply sunken, have no spines or tubercles on the peripore rims, but have a single large central tubercle within the

peripore and between the two perpendicular canals; the peripore is thus reduced to a moat-like channel around the central tubercle (Pl. 72, fig. 11; text-fig. 5b). *S. insuliporus* sp. nov. has dipopores which completely lack a peripore; only the central tubercle and pair of perpendicular canals remain (Pl. 73, fig. 8; text-fig. 5c). The dipopores of all species of *Sphaeronites* that we have examined fall into one or other of these three types which are used to distinguish three subgenera: *Sphaeronites* s.s., *Peritaphros* Paul, 1973, and *Ataphros* subgen. nov. Stratigraphically *Sphaeronites* (Arenig–Llanvirn) precedes *Peritaphros* (Llandeilo–Ashgill) which in turn precedes *Ataphros* (Ashgill). We recognize the following species of *Sphaeronites*:

**Sphaeronites* (*Sphaeronites*) *pomum* (Gyllenhaal, 1772); upper Arenig–lower Llanvirn, Sweden.

S. (S.) minor sp. nov.; upper Arenig, Sweden.

**Sphaeronites* (*Peritaphros*) *globulus* (Angelin, 1878); Llandeilo, Sweden.

S. (P.) pauciscleritatus sp. nov.; Caradoc, Norway.

S. (P.) variabilis sp. nov.; upper Caradoc–lower Ashgill, Sweden.

S. (P.) litchi (Forbes, 1848); lower-middle Ashgill, Wales.

S. (P.) pyriformis (Forbes, 1848) middle Ashgill, Wales.

S. (P.) sp. A.; lower Ashgill, Wales.

**Sphaeronites* (*Ataphros*) *insuliporus* sp. nov.; lower Ashgill, Wales.

* Denotes type species.

In addition to these there are possible forms of *S. (P.) globulus* and perhaps another new species from the middle Ordovician of the Baltic States which are the subject of study by Professor Hecker. These undoubtedly also belong to *Sphaeronites* as understood here. Thus *Sphaeronites* is an exclusively Ordovician genus known only from the Baltic Province and, in the late Ordovician, from Wales. *Sphaeronites* was used as a catch-all generic name and a very large number of species has been included within it at one time or another. We cannot list all these here, but we draw attention to the following more recently described species, which, in our opinion, do not belong in *Sphaeronites*:

Sphaeronis [sic] *jenhochiaensis* Sun, 1948 (p. 7) from China has the anus as much as 25 mm from the mouth and cannot be a *Sphaeronites* as we define the genus.

Sphaeronites globulus Termier and Termier, 1950 (pl. 228, fig. 1) from Algeria. The oral area is unknown and the specimen appears to be unidentifiable to judge from the illustration.

?*Sphaeronites* sp. Chauvel, 1966 (p. 65, pl. 2, fig. 12; pl. 4, fig. 10) from Morocco. Again the oral area is unknown, but this may well be an aristocystitid to judge from the dipopores.

Subgenus *Sphaeronites* (*Sphaeronites*)

Type species. *Echinus pomum* Gyllenhaal, 1772.

Diagnosis. A subgenus of *Sphaeronites*—bearing oval or rounded dipopores with blunt spines or tubercles on the rims between deeply sunken peripores; with flat or slightly convex peripore floors.

Sphaeronites (*Sphaeronites*) *pomum* (Gyllenhaal, 1772)

Plate 72, figs. 1, 2; Plate 73, fig. 6; text-figs. 5A, 17B, 24.

- 1945 *Sphaeronites pomum* (Gyllenhaal); Regnéll, p. 161, pl. 1, figs. 2, 3, 5; pl. 11, figs. 6–9, 12; pl. 12, figs. 2–4, 6; pl. 13, fig. 2; text-figs. 1:1–3; 19:1–3, 7–9; 20–21.
- 1948 *Sphaeronites pomum* (Gyllenhaal); Regnéll, pp. 13–14.
- 1960 *Sphaeronites pomum* (Gyllenhaal); Regnéll, p. 168.
- 1967 *Sphaeronites pomum* (Gyllenhaal); Kesling, p. S243, fig. 142: 1b, non fig. 142: 1a (= *S. globulus*).
- 1972 *Sphaeronites pomum* (Gyllenhaal); Paul, p. 25, pl. 5, fig. 2.
- 1973 *Sphaeronites* (*Sphaeronites*) *pomum* (Gyllenhaal); Paul, p. 23.
- 1978 *Sphaeronites pomum* (Gyllenhaal); Paul, p. 283.

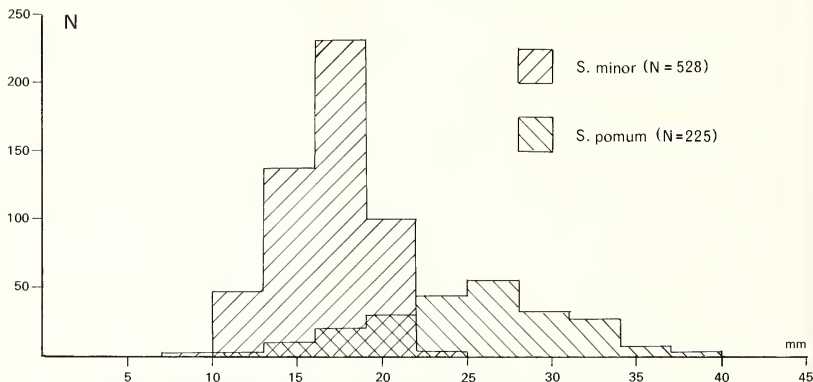
For a complete synonymy see Regnéll (1945, p. 161). We have only listed references since that paper.

Diagnosis. A species of *Sphaeronites* s.s. with large theca (reaching 35–40 mm diameter); diplopores with well-developed peripore rims which bear short spines abundantly; four to five diplopores per mm².

Types. Regnéll (1945, p. 162) selected a neotype (RM Ec2781) from Orthoceras Limestone, Kinnekulle, Västergötland, as Gyllenhaal's original material is apparently lost. However, Gyllenhaal's original description and figures are excellent and leave no doubt about which species was described in 1772.

Material. Hundreds of specimens from Kinnekulle Mountain and Öland, Sweden.

Horizons and localities. Regnéll (1945, pp. 167, 168) lists known localities. It is probable that some from Kinnekulle also refer to *S. (S.) minor* sp. nov. Our material comes from Österplana, Västergötland and from Södra Möckleby, Öland.



TEXT-FIG. 23. Frequency distribution of thecal diameter in *Sphaeronites (Sphaeronites) minor* sp. nov. and *S. (S.) pomum* from Österplana, Kinnekulle Mountain, Västergötland, Sweden. Note the wider range of sizes in *S. (S.) pomum*. Thecal diameter (mm), against number of individuals (N).

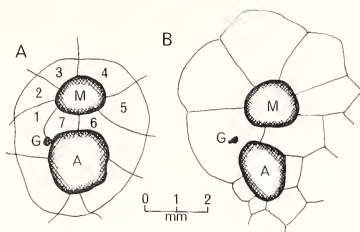
Description. Theca: spherical generally with a small oral platform and variable attachment area aborally. Often reaching 35–40 mm diameter (text-fig. 23) and with a very rough prickly surface when well preserved (pl. 72, figs. 1, 2).

Plates: numerous (as many as 450 plates estimated in a 35 mm diameter theca), small (mean area 7–9 mm²), and irregularly arranged. Plates are added during growth, but distinct generations of plates are not usually recognizable. Each plate bears numerous diplopores, although a narrow pore free zone may occur around the margin of the plates in some examples. All plates are slightly tumid so that the sutures are weakly impressed.

Diplopores (text-figs. 5A, 17B): densely packed over the theca. Peripores oval or rounded with flat or only slightly convex floors. Peripores reach 0.35–0.40 mm across with a pair of pores 0.05 mm in diameter set 0.2–0.35 mm apart. Peripore rims are well developed with prominent spines or tubercles developed at the junctions of three rims (text-fig. 5A). Spines reach 0.25 mm long on well-preserved examples from Öland (Pl. 72, figs. 1, 2), but are abraded on most examples either before deposition or, more commonly, as a result of weathering. The best-preserved examples display the prickly surface so well illustrated by Gyllenhaal (1772, pl. 8, fig. 3).

Oral surface (text-fig. 24): a small almost inconspicuous oral platform reaches 6 mm long (anterioposterior dimension) by 5 mm, but is usually a little smaller. The peristome is semicircular, small (2.0 mm by 2.5 mm) and covered by six palatal plates in rare examples. Ambulacral facets are rarely discernible. The periproct is small, circular, reaches 2 mm in diameter and is separated from the mouth by 0.4–0.5 mm. The gonopore is rarely detectable, but a small circular pore 0.15 mm in diameter is present in the usual position in SM A74827. A hydropore has not yet been confirmed.

TEXT-FIG. 24. Camera lucida drawings of the oral area of *Sphaeronites* (*Sphaeronites*) *pomum*. A, PMO A35283, upper *Sphaeronites* bed, Södra Möckleby, Öland, Sweden; B, SM A85676, *S. pomum* bed, Österplana, Kinnekulle, Sweden. 1–7, circum-oral plates; A, anus; G, gonopore; M, mouth.



Internal structures: unknown. All the calcite-filled examples that we have ground down in the aboral area of the theca failed to yield any evidence of the hollow internal spine known in several species of *Peritaphros*.

Attachment: direct, by a variable attachment area. The only specimens still attached to their substrates are always attached to other specimens of *S. (S.) pomum*. Sections through these show that plates of the attachment area are only half as thick as the main thecal plates. Other attachment areas indicate that *S. (S.) pomum* lived on orthoconic cephalopods and other shells in life.

Remarks. Gyllenhaal's original illustrations (refigured in Regnéll 1945, fig. 1: 1–3) show quite clearly the very prickly surface of his species. We have confined our interpretation of this species to those forms which exhibit this very rough surface. In Västergötland another species with a smaller and smoother test occurs which is described below as *S. (S.) minor* sp. nov. Detailed comparisons of the two species are presented after the description of the new form.

Sphaeronites (*Sphaeronites*) *minor* sp. nov.

Plate 72, figs. 3, 7, 8; text-figs. 9, 17A, 25.

1972 *Sphaeronites* sp. nov. Paul, p. 25, pl. 5, fig. 1.

1973 *Sphaeronites* (*Sphaeronites*) sp. A, Paul, p. 23.

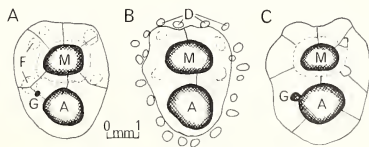
1978 *Sphaeronites minor* Paul, p. 283 (*nomen nudum*).

Diagnosis. A species of *Sphaeronites* s.s. with small theca (usually less than 25 mm at most); diplopores with well-developed peripore rims which bear occasional weak tubercles; about six diplopores per mm².

Types. Holotype SM A35313 (Pl. 72, figs. 3, 8), numerous paratypes (PMO, RM, SM, and authors' collections).

Material. Hundreds of specimens, all from Kinnekulle.

Horizons and localities. Lower (Grey) Asaphus Limestone (upper Arenig or possibly lowermost Llanvirn) of Kinnekulle Mountain, Västergötland, Sweden, where specimens occur in densities up to 5,000 per m². We have examined many hundreds of specimens from the *minor* bed and the overlying *pomum* bed at Kinnekulle. So far we have not found a single example of *pomum* in the *minor* bed or vice versa.



TEXT-FIG. 25. Camera lucida drawings of the oral area of *Sphaeronites* (*Sphaeronites*) *minor* sp. nov. A, SM A85644, B, SM A85618, C, SM A85629, all from *S. minor* bed, Österplana, Kinnekulle, Sweden. A, anus; D, diplopores; F, ambulacral facets; G, gonopore; M, mouth.

Description. Theca: globular to pyriform, depending on the size of the attachment area. Small, usually less than 20 mm diameter, rarely if ever exceeding 25 mm (text-fig. 23). Small raised oral platform and variable aboral attachment area.

Plates: numerous (300–400 estimated in larger thecae), irregularly arranged and small (usually only 4–5 mm² in area, largest 7 mm²). Each plate bears numerous diplopores, forty present on one plate which measures 2 × 3 mm.

Diplopores (text-fig. 17A): very densely and evenly developed over the theca, frequently crossing plate sutures. Peripores oval or polygonal (Pl. 72, fig. 7), the shape usually depending on adjacent diplopores because of the very dense packing. Peripore floor flat or gently convex, without a central tubercle. Peripores reach 0.25–0.30 mm across and contain a pair of pores 0.04 mm in diameter set about 0.2–0.3 mm apart. Peripore rims generally narrow and flat-topped. Where they meet, small blunt tubercles are sometimes developed, but they never form the spines characteristic of *S. (S.) pomum*. As a result the test surface appears to be much smoother than that of *S. (S.) pomum*.

Oral surface (text-fig. 25): the small oral platform reaches 4 × 3.5 mm and contains a semicircular to subquadrangular peristome 1.0 × 1.5 mm. Ambulacral facets are indistinct and close to the peristome border (Pl. 72, fig. 7). Palatals unknown. The periproct is circular, up to 1.5 mm in diameter and separated from the mouth by a calcite ridge 0.4–0.5 mm wide. In the holotype the peristome is smaller than the periproct, but the reverse is the case in SM A35315. Both orifices are surrounded by a smooth diplopore-free area which forms the raised oral platform (Pl. 72, fig. 7). Anal plates not preserved on any example we have examined. The gonopore is a small circular pore to the left of the peristome and periproct and midway between them. A hydropore has not been detected with certainty, but a slit-like impression (which might be a fortuitous crack) occurs between the peristome and periproct on the holotype. It is 0.3 × 0.03 mm.

Internal structures: as in *S. (S.) pomum* we have been unable to detect any internal spine.

Attachment: direct, by a variable attachment area. Again the only examples still attached occur epifaunally on other specimens of *S. (S.) minor*. Other substrates were the same as those of *S. (S.) pomum*.

Remarks. Although the presence of *S. (S.) minor* has been detected before, it has generally been included within *S. (S.) pomum* s.l., Regnéll (1945, p. 166) summarized the situation and concluded: 'Anyhow, it is evident that *Sphaerionites pomum* in typical development was preceded by a smaller form which must be regarded as conspecific, however. Since there are no really distinguishing features, and variations in size are too vague to be used for diagnostic purposes, there is no reason to denote the smaller specimens by a separate name'.

In the absence of any diagnostic character other than size it is wise to refrain from erecting new species, as Prof. Regnéll argued. However, we believe that the higher diplopore density, smoother

EXPLANATION OF PLATE 72

Figs. 1–2. *Sphaerionites (Sphaerionites) pomum* (Gyllenhaal), Asaphus Limestone, Södra Möckleby, Öland, Sweden. Two small examples from the lower *Sphaerionites* bed which reveal the characteristic prickly surface of *S. (S.) pomum*. 1, PMO A35326; 2, PMO A35320.

Figs. 3, 7, 8. *Sphaerionites (Sphaerionites) minor* sp. nov., Orthoceras Limestone, Kinnekulle Mountain, Västergötland, Sweden. 3, lateral and 8, oral views of the holotype, SM A35313, near Råbäck. 7, oral view of paratype, PMO A37044, Österplana, which shows details of the diplopores and the oral platform.

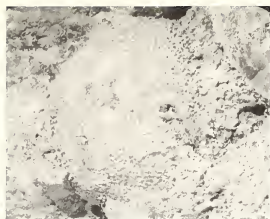
Figs. 4, 14. *Sphaerionites (Peritaphros) litchi* (Forbes), Sholeshook Limestone, Sholeshook, South Wales. 4, oral view of PMO A35439, showing the oral platform and cover plates. 14, lateral view of a latex of the lectotype, IGS GSM 7431, showing the characteristic diplopores.

Figs. 5, 6, 10. *Sphaerionites (Peritaphros) variabilis* sp. nov., Boda Limestone, Dalarna, Sweden. 5, lateral and 10, oral views of the holotype, SGU, Gulleråsens Lissberg. 6, lateral view of paratype, RM Ec26516, Osmundsberget.

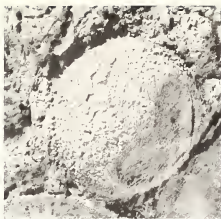
Figs. 9, 12, 13. *Sphaerionites (Peritaphros) pyriformis* (Forbes), Rhiwlas Limestone, near Bala, North Wales. 9, oblique view of lectotype, IGS GSM 102360, Rhiwlas. 12, lateral view of BM(NH) E16347; 13, lateral view of BM(NH) E16344; both from Llwyn-y-Ci and both showing the diplopores.

Fig. 11. *Sphaerionites (Peritaphros) globulus* (Angelin), Dalby Limestone, Bódahamn, Öland, Sweden. Oral view of RM Ec4193, showing ambulacral facets, gonopore, and characteristic diplopores.

All specimens whitened with ammonium chloride sublimate; all × 2.



1



2



3



4



5



6



7



8



9



10



11



12



13



14

thecal surface without short spines, and the consistently smaller size, when taken together, clearly indicate a distinct species.

Subgenus *Sphaeronites* (*Peritaphros*) Paul, 1973

1973 *Peritaphros* Paul, p. 21, text-fig. 13b.

Type species. *Sphaeronis globulus* Angelin, 1878, by original designation.

Diagnosis. A subgenus of *Sphaeronites* with generally polygonal diplopores which lack spines or tubercles on the ridges between the peripores but have a large, often H-shaped, central tubercle on the peripore floor between the perpendicular canals; the peripore is thus reduced to a moat-like channel around the central tubercle (Paul 1973, p. 23).

Sphaeronites (*Peritaphros*) *globulus* (Angelin, 1878)

Plate 72, fig. 11; text-figs. 5b, 17c, 26

- 1945 *Sphaeronites globulus* (Angelin); Regnéll, p. 168, pl. 11, figs. 10, 11; pl. 12, figs. 1, 3, 5; pl. 13, fig. 1; text figs. 19: 4, 5.
- 1948 *Sphaeronites globulus* (Angelin); Regnéll, p. 28.
- non 1950 *Sphaeronites globulus* Termier and Termier, pl. 228, fig. 1.
- 1967 *Sphaeronites pomum* Kesling, non Gyllenhaal, p. fig. 142: 1a.
- 1967 *Sphaeronites globulus* (Angelin); Kesling, p. S243, fig. 142: 1c-e [non fig. 142: 1f. (= *Eucystis*)].
- 1972 *Sphaeronites globulus* (Angelin); Paul, p. 25, pl. 5, fig. 3; text-fig. 7a.
- 1973 *Sphaeronites* (*Peritaphros*) *globulus* (Angelin); Paul, pp. 20-22, 24.
- 1978 *Sphaeronites globulus* (Angelin); Paul, p. 283.

Once again Regnéll (1945, p. 168) gives a complete synonymy prior to 1945 and we have only added more recent references.

Diagnosis. A species of *Peritaphros* with moderately large spherical theca (reaching 35-40 mm diameter); diplopores with a well-developed central tubercle which is flat-topped and level with the peripore rims; four to five diplopores per mm².

Types. Holotype, RM Ec4360, from the Dalby Limestone, the old harbour, Bödahamn, Öland.

Material. Several hundred specimens, mostly from Öland.

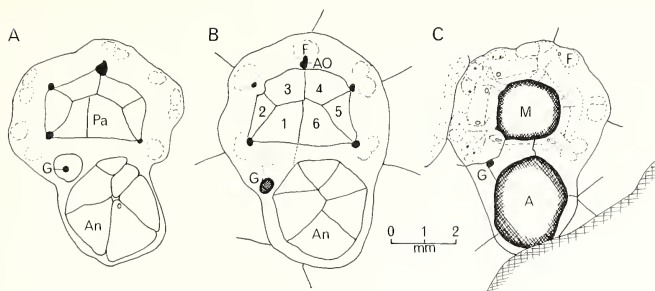
Horizons and localities. Regnéll (1945, p. 171) gives a thorough list of known localities, although the mention of 'Norway' probably refers to *S. (P.) pauciscleritatus* sp. nov. Most of our specimens come from the type locality in the Dalby Limestone of the old harbour at Bödahamn, Öland. *S. (P.) globulus* probably ranges through the lower half of the Caradoc.

Description. Theca: generally spherical with small oral platform and aboral attachment area. The theca reaches 35 mm diameter and the surface appears to be fairly smooth due to the flat-topped central tubercles of the diplopores.

Plates: fairly numerous (about 350 estimated in a 30 mm diameter theca), small to medium sized (mean area 7-8 mm²) and irregularly arranged. All bear numerous diplopores and none is tumid, the theca often having a regularly spherical outline (Pl. 72, fig. 11).

Diplopores (text-figs. 5b, 17c): densely packed and characteristic of the subgenus *Peritaphros* with a large, often H-shaped, central tubercle which is flat-topped and level with the peripore rims. Peripores reach 0.40-0.45 mm across, with a pair of pores about 0.1 mm in diameter and separated by 0.20-0.25 mm. Peripore rims are narrow and sharp edged.

Oral surface (text-fig. 26): a small oral platform is developed. It reaches 7 × 5 mm and includes the mouth and anus as usual. Almost invariably the mouth is covered by the six palatal plates and it reaches 2.5 × 3.0 mm. Ambulacral facets are often preserved (Pl. 72, fig. 11) and one or two occur per ambulacrum. Nine is the maximum number we have counted. The facets are small, close to the edge of the peristome, and food entered the mouth via minute ambulacral orifices. The anus is oval, up to 3 mm across and covered by an anal pyramid of six plates (Pl. 72, fig. 11). The mouth and anus are separated by about 0.5 mm in most specimens. The gonopore is a



TEXT-FIG. 26. Camera lucida drawings of the oral area of *Sphaerontes (Peritaphros) globulus*. A, SM A85681, B, SM A85689, C, SM A85701, all from the Dalby Limestone, Bödahamn, Öland, Sweden. 1–6, oral cover plates (palatals, Pa); A, anus; An, anal cover plates; AO, ambulacral orifice; F, ambulacral facet; G, gonopore; M, mouth.

small circular orifice, up to 0.5 mm in diameter and sometimes raised in a tubular protuberance adjacent to the anal pyramid and ambulacral facet 1 (e.g. Pl. 12, fig. 11). Of all species *S. (P.) globulus* and, to a lesser extent, *S. (P.) variabilis* sp. nov. have the best-preserved oral surfaces.

Internal structures: grinding down the aboral part of the theca has revealed a hollow internal spine which seems to be characteristic of the subgenus *Peritaphros*.

Attachment: direct by a small, usually flat, attachment area. We have seen no example still attached to its substrate.

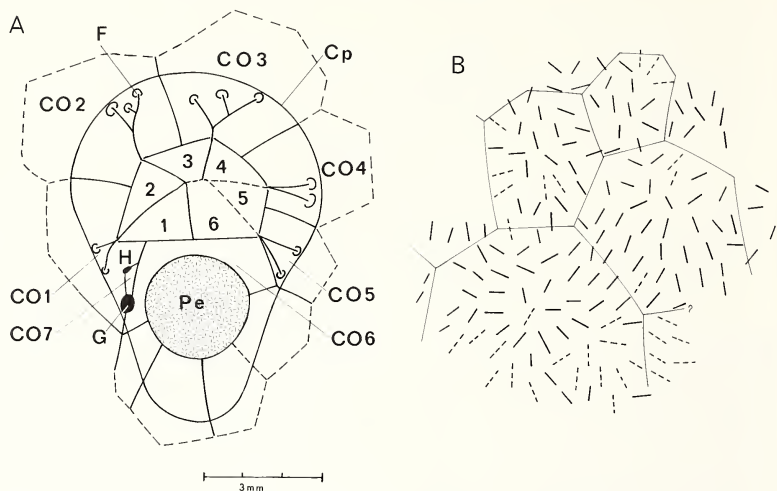
Remarks. Although *S. (P.) globulus* was the first species of *Peritaphros* to evolve, its diplopores are quite typical of the subgenus and already quite different from those of *S. (S.) minor* and *S. (S.) pomum*. The diplopore density is about the same as in the much older *S. (S.) pomum* and it seems that the main evolutionary change between the two species involved the type of diplopore. Once established, *Peritaphros* diplopores continued the trend towards lower densities. *S. (P.) globulus* occurs at Bödahamn in very large numbers accompanied by three other cystoid species which are also very common. They are *Echinosphaerites aurantium* (Gyllenhaal, 1772), *Caryocystites dubia* (Angelin, 1878), and *Lophocystites granatum* (Wahlenberg, 1818). Of these, *S. (P.) globulus* and *E. aurantium* are consistently better preserved and we have seen only one example of *S. (P.) globulus* without the oral and anal cover plates still in place (text-fig. 26C).

Sphaerontes (Peritaphros) pauciscleritatus sp. nov.

Plate 73, fig. 1; text-fig. 27

- 1865 *Echinosphaerites pomum* var. Kjerulf, p. 4 (*pars.* ?).
- 1879 *Echinosphaerites pomum* Kjerulf, pl. 11 (*pars.* ?).
- 1887 *Echinosphaerites aurantium* Brögger, p. 21.
- 1934 *Echinosphaerites aurantium* Störmer, p. 331.
- 1945 *Glyptosphaerites* sp. Regnéll, p. 25.
- 1945 *Sphaerontes globulus* (Angelin); Regnéll, pp. 161, 171 (*pars.* ?).
- 1948 *Echinosphaerites aurantium* (Gyllenhaal); Regnéll, p. 21.
- 1948 *Glyptosphaerites* sp. Regnéll, p. 21.
- 1948 *Sphaerontes pomum* Regnéll, p. 31 (*pars.* ?).
- 1953 Diploporite cystoid Störmer, p. 65.
- 1967 *Glyptosphaerites* sp. Kesling, p. S145, text-fig. 67.
- 1978 *Sphaerontes* Bockelie, p. 198, fig. 3a.
- 1978 *Sphaerontes pauciscleritatus* Paul, p. 283 (*nomen nudum*).

Diagnosis. A species of *Peritaphros* with large globular theca reaching 40–50 mm in diameter in adult specimens; thecal plates limited (fifty to sixty); diplopores polygonal (0.4×0.4 to 0.4×0.6 mm in adult specimens), average diplopore pore density 3.7 per mm^2 .



TEXT-FIG. 27. A, camera lucida drawing of the oral area of *Sphaeronites (Peritaphros) pauciscleritatus* sp. nov. Holotype, PMO 79687, Stage 4b β , Oslofjord. 1–6, oral cover plates (palatals); CO1–CO7, circum-oral plates; F, ambulacral facets; G, gonopore; H, hydriopore; Pe, peripore. B, traces of axes of diplopores in *Sphaeronites (Peritaphros) pauciscleritatus* sp. nov., PMO 79687, Stage 4b β , Oslofjord.

EXPLANATION OF PLATE 73

Fig. 1. *Sphaeronites (Peritaphros) pauciscleritatus* sp. nov., Lower Chasmops Limestone, Hareholmen, Ostoya, Baerum, Norway. Oral view of latex of paratype, PMO 90042, to show large size and characteristic polygonal diplopores.

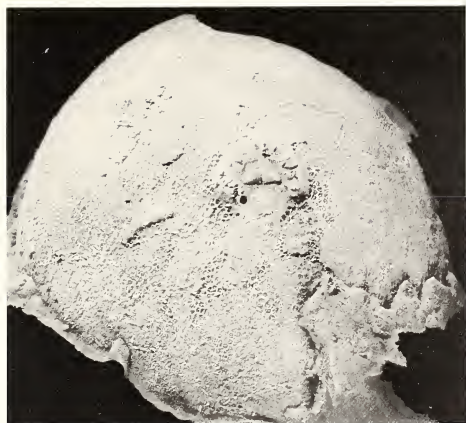
Figs. 2, 5, 8. *Sphaeronites (Ataphros) insuliporus* sp. nov., Sholeshook Limestone, Sholeshook, South Wales. 2, lateral and 5, oral views of the holotype, SM A85708. 8, detail of diplopores on SM A82024, to show lack of peripores characteristic of the subgenus *Ataphros*; latex, $\times 4$.

Figs. 3, 7. *Sphaeronites (Peritaphros) litchi* (Forbes), Sholeshook Limestone, Sholeshook, South Wales. 3, oblique oral view of SM A31230, a specimen with damaged plates which reveal the growth lines. 7, detail of diplopores on SM A31233 showing prominent central tubercles and moat-like peripores characteristic of the subgenus *Peritaphros*; $\times 6$.

Fig. 4. *Sphaeronites (Peritaphros)* sp. A. Dolhir Beds, Glyn Ceiriog, North Wales. Latex of SM A53853 to show very large diplopores; $\times 6$.

Fig. 6. *Sphaeronites (Sphaeronites) pomum* (Gyllenhaal), Orthoceras Limestone, near Råbäck, Kinnekulle, Västergötland, Sweden. Detail of diplopores on SM A52977, a weathered specimen showing the oval sunken peripores characteristic of the subgenus *Sphaeronites* s.s.; $\times 6$.

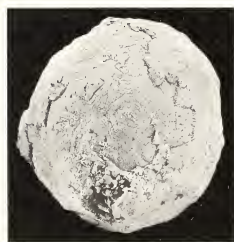
All specimens whitened with ammonium chloride sublimate; $\times 2$ unless otherwise indicated.



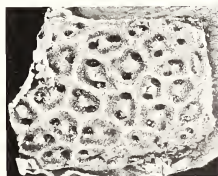
1



2



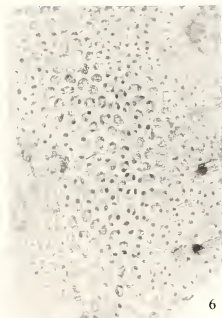
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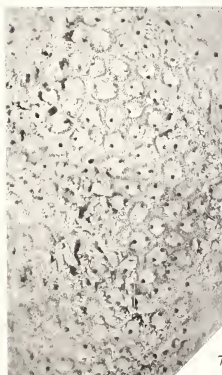
4



5



6



7



8

Derivation of name. From Latin *pauci* = few, and Greek *scleros* = skeletal plate.

Types. Holotype, PMO 79687; paratypes, PMO 6183, 90042, 90043, 90289, 90293, 90297, 90347, 90349, 90350, 90351.

Material available. Holotype and a dozen paratypes.

Horizon and locality. Middle part of lower Chasmops Limestone (= Stage 4b β), middle Caradoc, Oslo-Åsker District of the Oslo Region, Norway.

Description. Theca: globular, large, usually 30–50 mm in diameter in adult specimens; surface fairly smooth. Oral platform flat, slightly elevated. Attachment area variable.

Plates: not numerous (approximately fifty), fairly regularly arranged, usually pentagonal or hexagonal, each measuring about 10 × 10 mm in average specimens. The centre of individual plates is slightly elevated so that sutures are weakly impressed. Numerous diplopores are present on the thecal plates, about thirty-five occur on a plate which measures 4 × 5 mm (text-fig. 27b).

Diplopores: distributed over thecal surface, but only occasionally crossing plate sutures. In most cases, a narrow zone adjoining the plate sutures is devoid of peripores as in *S. (S.) pomum*. The periporal walls are generally high towards plate centre, decreasing towards the plate margins, which is also the case in *S. (S.) pomum*. In *S. (P.) globulus* the periporal wall is generally lower and slightly thicker. Peripores polygonal, often irregular pentagonal or hexagonal (Pl. 73, fig. 1). Peripore floors generally flat with a broad, constricted central tubercle. Peripores large, reaching 0.40 to 0.60 mm in major dimension (usually length) and contain a pair of pores 0.05 mm in diameter and set about 0.20 mm apart. Diplopore density averages 3.7 per mm² (110 measurements from eleven specimens, standard deviation 0.4 mm).

Oral surface (text-fig. 27a): a little below the external surface, the peristome appears elliptical, measuring 3.6 × 5.0 mm in the holotype and 3.3 × 5.0 mm in PMO 90042. In the holotype three of the six palatals are preserved; in PMO 90042 they are all well preserved (Pl. 73, fig. 1). Twelve ambulacral facets in the holotype (text-fig. 27a); two in radii I, IV, and V and three in radii II and III; branching either directly from corners of, or as sidebranches off major grooves. The ambulacral facets are indistinct, but appear to have been semicircular or kidney shaped. The periproct is circular in the holotype, 2.5 mm in diameter and separated from the peristome by a calcite ridge 0.2–0.3 mm wide. The periproct is usually larger than the peristome, but in the holotype the maximum dimensions are the same (3.1 mm). Both orifices are surrounded by a smooth, pear-shaped rim free of diplopores which form the oral platform. Six triangular anal plates cover the periproct in PMO 6183. The circular gonopore is usually large, being up to 1 mm in diameter in the largest specimens (Pl. 73, fig. 1). It is present left of the peristome and periproct, and often almost in contact with the central portion of the left side of the periproct. An elongated hydopore is located on the suture O1:O6 just adoral to the gonopore. The hydopore is 0.4 × 0.3 mm in PMO 90042.

Internal structures: the internal spine or remains of it have been found in several specimens.

Attachment: direct by a variable attachment area.

Remarks. *S. (P.) pauciscleritatus* has been known to occur in Norway since Kjerulf (1865), but has never been described. Kjerulf, who referred it to '*Echinospaerites pomum*', may have been aware of the presence of the diplopores. Subsequent authors, however, have referred it to *Echinospaerites aurantium*. This species is very distinctive because of its great size and relatively few, large plates.

Sphaeronites (Peritaphros) variabilis sp. nov.

Plate 72, figs. 5, 6, 10; text-figs. 6, 13, 17d, 28

1945 Cystoid; gen. et sp. indet. Regnéll, p. 183, pl. 15, fig. 1.

1972 *Sphaeronites* sp. nov. (Skälberget, Sweden) Paul, p. 25, pl. 5, fig. 4.

1973 *Sphaeronites (Peritaphros)* sp. B. Paul, pp. 20–22, 24, text-figs. 10–12.

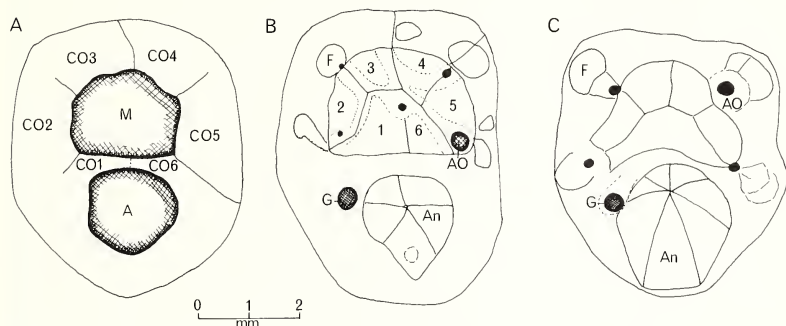
1978 *Sphaeronites variabilis* Paul, p. 283 (*nomen nudum*)

Diagnosis. A species of *Peritaphros* with theca generally higher than wide, with relatively few plates. Diplopores polygonal or rounded with wide, low rims and a central tubercle elevated slightly above the level of the rims. Pore density averages just over three diplopores per mm².

Types. Holotype, the well-preserved specimen (SGU unregistered) originally figured by Regnéll (1945, pl. 15, fig. 1), from Gulleråsen, Dalarna.

Material. Holotype and several dozen paratypes, PMO, RM, SM and authors' collections.

Horizons and localities. This species first appears in bedded limestones equivalent to the Skålberg Beds about 5 m below the top of the Fjäckå Shale on the south side of the quarry at Osmundsberget, Dalarna, Sweden. These specimens are larger than all younger individuals and not very well preserved. The bed has now been quarried away completely. Above the Fjäckå Shale, *S. (P.) variabilis* occurs through the lower half of the Boda Limestone. The species ranges from perhaps as low as the upper Onnian to perhaps as high as the lower Rawtheyan, but both limits are uncertain. Our specimens come from the Boda Limestone at Skålberg, Osmundsberget, Gulleråsen and Boda Church, Dalarna.



TEXT-FIG. 28. Camera lucida drawings of the oral area of *Sphaeronites (Peritaphros) variabilis* sp. nov. A, RM Ec25954; B, RM Ec25944; C, PMO A35423. All from the Boda Limestone, Osmundsberget (A) and Skålberg (B and C), Dalarna, Sweden. 1–6, oral cover plates (palatals); A, anus; An, anal cover plates; AO, ambulacral orifice; CO1–CO6, circum-oral plates; F, gonopore; M, mouth.

Description. Theca: variable in shape, pyriform, fusiform, or hemispherical, sometimes very irregular in shape (cf. Pl. 72, figs. 5, 6), with a fairly prominent oral platform and variable attachment area. Theca usually 15–25 mm in diameter, but reaching 50 mm high and 30 mm in diameter in the specimens from below the Fjäckå Shale at Osmundsberget. The surface is fairly smooth, but this has sometimes been enhanced by pressure solution (e.g. Pl. 72, fig. 5).

Plates: not very numerous (rarely, if ever, over seventy, certainly less than 100), arranged fairly regularly in four to six circlets of about ten plates, although the basal circlet has only seven. Plates polygonal in outline and moderately large, reaching an average area of 40 mm² in some specimens. Diplopores are developed on all plates.

Diplopores (text-fig. 17D): evenly distributed over the theca with a density of three per mm². Outlines polygonal or occasionally rounded, with the central tubercle projecting above the level of the peripore rims, which are wider than in any other species except *S. (P.) pyriformis* (Forbes). Peripores relatively large, exceeding 0.5 mm across, with a pair of pores 0.07 mm in diameter and up to 0.45 mm apart.

Oral surface (text-fig. 28): a generally prominent oral platform is present which reaches 10.2 × 6.5 mm and contains both the peristome and periproct as usual in *Sphaeronites* (Pl. 72, fig. 10). Peristome reaches 2.5 × 3.6 mm and is generally covered by the six palatals (text-fig. 28). The ambulacral facets are close to the edge of the peristome, small, and one or two occur per ambulacrum. At least five examples we have seen lacked facets in ambulacrum III, an exceedingly rare feature. The periproct is circular, up to 3 mm in diameter and covered by six anals. The peristome and periproct are separated by at least 0.5 mm and more than 1 mm in some specimens. The circular gonopore is relatively large and reaches 0.7 mm diameter. A smaller hydropore 0.3–0.4 mm across is also present in some specimens between the gonopore and the peristome.

Internal structures: an aboral internal spine, which is partly hollow and partly C-shaped in section, occurs in several specimens we have sectioned, including the one illustrated in text-fig. 6.

Attachment: direct by a variable attachment area which is generally oval in outline. A few examples are known still attached to other cystoids and in one case to a crinoid stem. As usual, the shape and size of the attachment area reflect the nature of the substrate.

Remarks. As the name implies, *S. (P.) variabilis* is not characterized by a regular thecal shape. Of the other species, only *S. (P.) pyriformis* displays anything like the variability in thecal shape found in *S. (P.) variabilis*. Specimens also vary in size and those from below the Fjåcka Shale at Osmundsberget are consistently much larger than all later examples. It is possible that they represent a distinct species, but so far we have been unable to find any other character than size on which to distinguish them. Quite possibly the bed represents a population which became fully grown in stable conditions before being buried, whereas most of the later examples died relatively young on the unstable slopes of the Boda bioherms. For the present it seems to us best to include all these specimens in one species. The holotype, however, is from the Boda Limestone flank facies.

Sphaeronites (Peritaphros) litchi (Forbes, 1848)

Plate 72, figs. 4, 14; Plate 73, figs. 3, 7; text-figs. 17F, 29

1973 *Sphaeronites (Peritaphros) litchi* (Forbes); Paul, p. 23, pl. 1, figs. 2, 7-9, 12-15; pl. 2, figs. 1, 2; pl. 10, fig. 9; text-figs. 15, 16.

1978 *Sphaeronites litchi* (Forbes); Paul, p. 283.

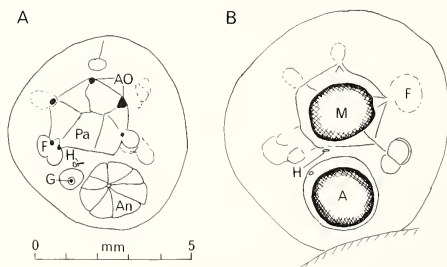
For a full synonymy of this species see Paul 1973, p. 23.

Diagnosis. A species of *Peritaphros* with fusiform to globular theca; polygonal diplopores with very prominent central tubercles elevated above the level of the sharp-crested peripore rims; about two and a quarter diplopores per mm².

Type. GSM 7431a (Pl. 72, figs 14), the original of Forbes 1848, pl. 21, figs. 2c, d, was selected as lectotype by Paul 1973, p. 23.

Material available. About twenty more or less complete thecae, GSM, HM, SM, PMO.

Horizons and localities. The lectotype is from the Sholeshook Limestone (Ashgill, zones 2-5) at Sholeshook, near Haverfordwest, South Wales. *S. (P.) litchi* occurs between 13 and 37 m in the Sholeshook section. It also occurs



TEXT-FIG. 29. Camera lucida drawings of the oral area of *Sphaeronites (Peritaphros) litchi*. A, SM A85706, B, PMO A37047, both from the Sholeshook Limestone, Sholeshook, South Wales. A, anus; An, anal cover plates; AO, ambulacral orifices; F, ambulacral facet; G, gonopore; H, hydropore; Pa, palatal plates.

in the Sholeshook Limestone at Llandowror, South Wales and the Rhiwlas Limestone (Ashgill, zone 5) at Rhiwlas, near Bala, North Wales.

Description. Theca: inflated fusiform to pyriform and up to 45 mm in height and 35 mm in diameter. Peristome and periproct close together on a small oral prominence. Usually with an attachment area up to half the ambital diameter.

Plates: precise arrangement unknown, of two generations, the primaries reaching 6–7 mm in major dimension. All plates except those forming the attachment area, covered with evenly developed diplopores which give the surface a rough appearance.

Diplopores (text-fig. 17f): polygonal in outline, with narrow, sharp-crested peripore rims and a very prominent central tubercle which rises 0.20–0.25 mm above the plate surface (Pl. 73, fig. 7). Peripore tubercle often H-shaped. Pores 0.10–0.17 mm in diameter and 0.25–0.33 mm apart. Diplopore density averages 2.26 per mm².

Oral surface (text-fig. 29): a prominent oral platform is developed which reaches 9 × 7 mm in the largest examples and contains the mouth and anus (Pl. 72, fig. 4). Peristome 2.5 × 2 mm, anus more rounded and 2–3 mm in diameter. Six plates surround the mouth which is separated from the anus by 0.25–0.4 mm. Mouth covered by the usual six palatal plates and the anus by a pyramid of eight anals (Pl. 72, fig. 4; text-fig. 29a). A small circular gonopore 0.2 mm in diameter is present in SM A85706. Sometimes it is raised as a tubercle (Pl. 72, fig. 4).

Internal structures: a tubular aboral internal spine is preserved in GSM 102380. The tube is 3.5 mm in diameter and 8.6 mm long.

Attachment: direct by a variable aboral attachment area, usually from a fifth to nearly half the maximum diameter (Pl. 72, fig. 14).

Remarks. A full account of the nomenclatural history of this species is given by Paul (1973, pp. 23–25). The species is very distinctive and can be recognized by the prominent central tubercle in the diplopores which gives the external surface a very rough appearance.

Sphaeronites (Peritaphros) pyriformis (Forbes, 1848)

Plate 72, figs. 9, 12, 13; text-figs. 17e, 30

1973 *Sphaeronites (Peritaphros) pyriformis* (Forbes); Paul, p. 25, pl. 1, 3, 4, 6, 10, 11; text-fig. 17. [See for full synonymy].

Diagnosis. A small species of *Peritaphros* with pyriform to cylindrical theca not more than 15 mm high; oval to subangular diplopores with flat-topped central tubercles, diplopore density averaging two and a half diplopores per mm².

Types. GSM 102360 (Pl. 72, fig. 9), the original of Forbes 1848, pl. 21, figs. 1a–b, was selected as lectotype by Paul 1973, p. 26. GSM 102361–2 are paralectotypes.

Material available. About twenty more or less complete thecae. GSM, BM(NH), SM, PMO.

Horizons and localities. Rhiwlas Limestone (Ashgill, zone 5) at Rhiwlas and Llwyn-y-Ci, near Bala, North Wales.

Description. Theca: conical (Pl. 72, figs. 12, 13) to fusiform or irregular, bent through 180° in one example. Always small, up to 13 mm high and 10 mm in diameter. Peristome and periproct close together on oral prominence which is almost as wide as the entire theca (Pl. 72, fig. 9). Attached directly by a relatively large attachment area.

Plates: usually between twenty-five and thirty-five, arranged in four circlets of seven or eight plates each, all of one generation. Plates reach 5 mm in maximum dimension and all bear diplopores.

Diplopores (text-fig. 17e): rather sparsely developed and hence frequently oval in outline (Pl. 72, figs. 9, 12, 13). With broad flat-topped peripore rims and large flat-topped central tubercle level with the peripore walls. Less evenly developed than in other species of *Sphaeronites* s.l. Diplopore density averages 2.6 per mm².

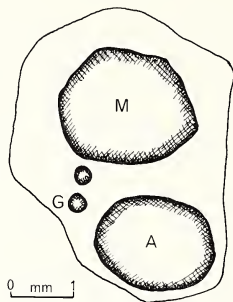
Oral surface (text-fig. 30): peristome small, oval to rounded, 2.5 × 1.9 mm in the lectotype. Surrounded by CO1–CO6, CO7 not confirmed. Apparently only one ambulacral facet per ambulacrum; facets rounded and 0.80–0.85 mm in diameter in GSM 102362 and the lectotype. Facets generally poorly preserved and difficult to detect. Palatal and anal plates not preserved (in contradiction to Forbes's 1848, pl. 21, fig. 1b). Periproct

rounded-oval, 1.9 mm in diameter in lectotype. Gonopore a small circular pore 0.5 mm in diameter to the left of the peristome and periproct and developed across a plate suture between CO1 and CO6 or CO7; precisely which is uncertain. Double in BM(NH) E16347. Hydropore not detected.

Internal structures: unknown.

Attachment: direct by an aboral attachment area which may be the widest part of the theca. Attachment is often oblique to the ad-aboral axis and may extend up one side of the theca (e.g. BM(NH) E16345). BM(NH) E16346 attached to a crinoid root structure.

TEXT-FIG. 30. Camera lucida drawing of the oral area of *Sphaeronites* (*Peritaphros*) *pyriformis* BM(NH) E16347, Rhiwlas Limestone, Llwyn-y-Ci, North Wales. A, anus; G, gonopore; M, mouth.



Remarks. *S. pyriformis* is known from a moderate number of specimens, all of which are smaller than those of any other species of *Sphaeronites* s.l. This may reflect an environmental peculiarity of the Rhiwlas Limestone; all specimens could have become detached and buried before maturing; or *S. pyriformis* could be a genuinely small species. In either event available material is quite distinct from all other species on the basis of size alone. Forbes's original type set contained four specimens of which one, GSM 7432, is much larger and has angular diplopores with very prominent central tubercles. On these grounds Paul (1973, p. 27) assigned this specimen to *S. (P.) litchi*. We have since found at least one more specimen of *S. (P.) litchi* in the Rhiwlas Limestone. The possibility that *S. (P.) pyriformis* represents the juvenile stage of *S. (P.) litchi* still remains and will continue to do so until a really small example of the latter is found.

Sphaeronites (*Peritaphros*) sp. A

Plate 73, fig. 4

1972 *Sphaeronites* sp. Paul, p. 25.

1973 *Sphaeronites* (*Peritaphros*) sp. A, Paul, p. 27, pl. 1, fig. 5.

Material available. A single specimen, SM A53853, which is an external mould of a small fragment of theca.

Horizon and locality. Dolhir Limestone (Ashgill, zone 2) from an old tram cutting ENE of Coed-y-Glyn-Isaf, Glyn Ceiriog, North Wales.

Description. A small portion of theca 6.5 × 4.3 mm which preserves about twenty-six diplopores (Pl. 73, fig. 4).

Diplopores: large for *Peritaphros* (1.1–1.5 mm in major dimension), polygonal, with a relatively weak central tubercle. Peripore rims strongly developed but not flat-topped. Diplopore density averages 1.5 per mm², which is nearly half that of any other species of *Peritaphros*.

All other features of morphology unknown.

Remarks. The diplopores of SM A53853 show closest similarities to those of *Peritaphros* spp., but they are much larger and much less densely developed than in any described species. Most

likely this small fragment represents a new species but it is unsuitable to become the type of a new species.

Subgenus *Sphaeronites* (*Ataphros*) subgen. nov.

Type species. *Sphaeronites* (*Ataphros*) *insuliporus* sp. nov.

Diagnosis. A subgenus of *Sphaeronites* with diplopores which lack any peripores, the perpendicular canals opening on either side of a small central tubercle.

Sphaeronites (*Ataphros*) *insuliporus* sp. nov.

Plate 73, figs. 2, 5, 8; text-figs. 5c, 31, 32

1973 *Diploporita incertae sedis* sp. D, Paul, p. 61, pl. 10, figs. 3, 5, 6; text-fig. 38b.

Diagnosis. As for the subgenus which is monotypic.

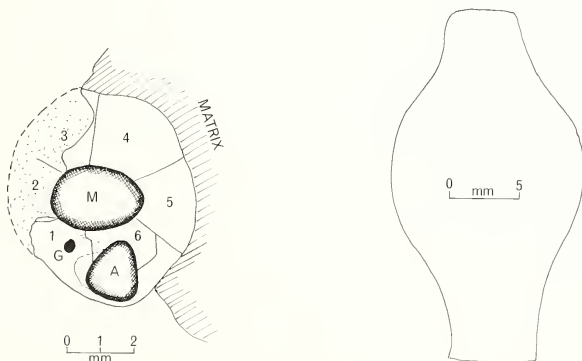
Types. Holotype SM A85708, a nearly complete theca. Paratypes SM A82024, 5, two small fragments of external mould.

Material. The three specimens listed above.

Horizons and localities. Sholeshook Limestone (Ashgill, zones 2-5) between 11.6 and about 35 m in the railway cutting at Sholeshook, South Wales. The holotype came from a loose block between 34 and 37 m.

Description. Theca: fusiform in the holotype (Pl. 73, fig. 2) which is slightly crushed and measures 29 mm high by about 15 mm in maximum diameter which occurs about two thirds of the height (text-fig. 32). Both ends of the theca are extended to form the oral platform and the attachment area.

Plates: relatively few, probably less than fifty and apparently arranged in six circlets. They reach 6-7 mm across. All are apparently very thin, about 0.35 mm thick, which may account for the rarity of the species and the fragmental nature of the first specimens found. All are covered with diplopores.



TEXT-FIG. 31 (left). Camera lucida drawing of the oral area of *Sphaeronites* (*Ataphros*) *insuliporus* sp. nov. Holotype, SM A85708, Sholeshook Limestone, Sholeshook, South Wales. 1-6, circum-oral plates; A, anus; G, gonopore; M, mouth.

TEXT-FIG. 32 (right). Camera lucida drawing of the thecal outline of the holotype of *Sphaeronites* (*Ataphros*) *insuliporus* sp. nov., SM A85708.

Diplopores (text-fig. 5c): evenly, but rather sparsely developed for a species of *Sphaeronites*. All lack peripores (Pl. 73, fig. 8), but the small perpendicular canals, 0.08 mm in diameter in the holotype, lie on either side of a central tubercle and are about 0.1 mm apart centre to centre. The central tubercles of the diplopores resemble those of *Peritaphros* spp.

Oral surface (text-fig. 31): a prominent, flat-topped oral platform about 3 mm in diameter occurs (Pl. 73, fig. 5). The peristome and periproct lie close together within this (Pl. 73, fig. 5) indicating that it is a species of *Sphaeronites* as here defined. A small circular gonopore 0.25 mm in diameter and possibly a slit-like hydropore lie between the mouth and anus and to the left. The mouth is oval, about 3×2 mm, while the anus is more irregular and about 2 mm across. The oral area is deeply weathered which reveals plate sutures, but not ambulacral facets. The usual six plates make up the peristome frame.

Internal structures: unknown.

Attachment: direct by a small rather expanded attachment area about 7.5 mm across.

Remarks. Paul (1973, p. 61) first reported this cystoid on the basis of two incomplete external moulds which had unusual diplopores. He remarked that the diplopores in some ways resembled those of *Peritaphros* spp., but was unable to say more. By extraordinary good fortune we are now able to identify this species. While collecting at Sholeshook in 1974 we found a cystoid in a small piece of rock which split so that most of the theca remained in one part, but a small fragment attached to the other. On decalcifying the small part we discovered that it had diplopores like the hitherto unidentifiable fragments (SM A82024–5). Meanwhile, the main body of the theca had the oral area exposed and confirmed the thecal shape and systematic affinities of the specimen. Without both parts, one preserved as the original theca and the other now as an external mould, we would not be able to identify this specimen.

The diplopores are so distinctive that although this is clearly a *Sphaeronites* on the basis of the arrangement of orifices and plates in the oral platform, it cannot be assigned to either *Sphaeronites* s.s. or *Peritaphros*. Hence we define a new subgenus, *Ataphros*, in allusion to the lack of peripores in this species.

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HOMOLOGIZATIONS OF SKULL ROOFING BONES BETWEEN TETRAPODS AND OSTEOLEPIFORM FISHES

by ULF J. BORGÉN

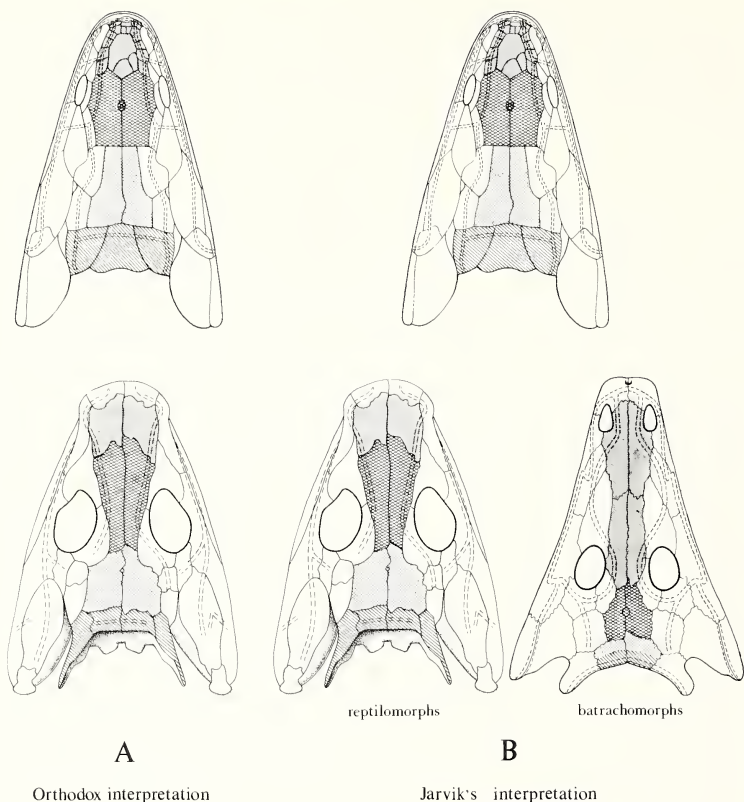
ABSTRACT. The assumption of a constant positional relationship between dermal bones and endocranial structures, which constitutes the basis for the main arguments of proponents of three suggested solutions concerning the correct homologies of the medial exocranial bones of tetrapods and osteolepiform fishes, is discussed and criticized. It is shown that, by disregarding this assumption, these homologies are easily understood. The five medial, often paired exocranial bones present in most tetrapods, except in those where the postparietals are missing, are the same five medial bones that are present in osteolepiforms if the nasals and postrostrals in these forms are fused. The homologies of the exocranial bones in *Ichthyostega*, and the phylogenetic position of this form are also discussed.

SINCE the 1930s a division of opinion has split the field of lower vertebrate palaeontology and comparative anatomy into two camps. In general this disagreement concerns the homologies, and thus the correct terminology of the bones in the exocranial roof of the crossopterygian fishes, but the core of the problem is in the homologies between tetrapods and crossopterygians of the bones along the midline of the exocranial roof. The background to this conflict has been reviewed previously by, for example, Jarvik (1967, p. 181) and Parrington (1967, p. 231), and thus it is necessary here only to summarize the alternatives.

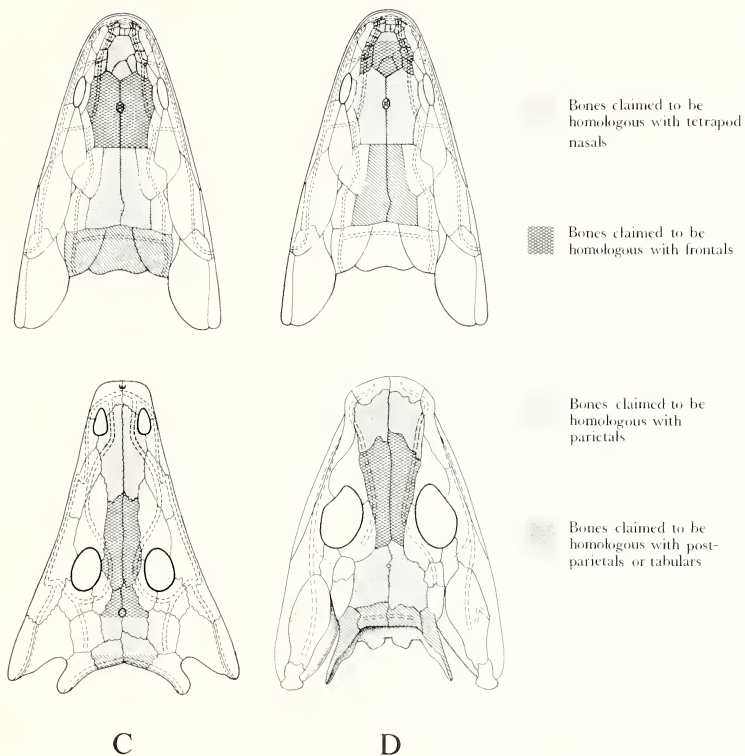
One alternative (text-fig. 1A), which like Westoll (1943, table 1) I refer to as 'the orthodox terminology', was used by early authors such as Traquair (e.g. 1884), Smith Woodward (e.g. 1891, p. 318, fig. 47), Watson (e.g. 1926a, p. 196, fig. 2), Sæve-Søderbergh (e.g. 1933, p. 9), Moy-Thomas (e.g. 1935, figs. 1, 2), and Westoll (e.g. 1936, figs. 1, 3). To my knowledge, this alternative has not been argued for in its original form by any recent authors. However, a modified version (text-fig. 1B) has been argued for most strongly by Jarvik (1967). More or less modified versions of the orthodox terminology are mainly used today by continental European authors such as Lehman (e.g. 1959, p. 110, fig. 49), Jessen (e.g. 1966), Jarvik (e.g. 1967), and Bjerring (e.g. 1979), and also by some Australian authors such as Young and Gorter (1981).

Alternative terminologies (text-figs. 1C, D) were suggested respectively by Sæve-Søderbergh (1932, figs. 16A, 18, table 2, p. 92) and Westoll (1936, p. 166; 1938, 1940, p. 71; 1943, p. 79). To my knowledge Sæve-Søderbergh's terminology is not now used by any authors. Westoll's solution were supported by, for example, Romer (1937, p. 52; 1941, p. 150) and Parrington (1956, 1967). The terminology following from Westoll's views is used today mainly by authors in Great Britain and the U.S.A., and also by some Russian authors (Vorobyeva 1977).

This dispute needs to be discussed for several reasons. 1. In their arguments, the proponents of the different alternatives have employed general assumptions concerning the positional relationship between the endocranium and dermal bones in general, with very far-reaching impacts on the methods of comparative vertebrate anatomy. These assumptions thus need to be checked. 2. Osteolepiforms and stegocephalians presumably include links in the transition between tetrapods and the assemblage that we call fishes. Since the names of the main cranial roof bones are defined in man, and their homologies among tetrapods are generally accepted, it is necessary to clarify what happened to these bones at this transition, in order to place correct names on these bones in fishes. Obviously this knowledge is important when establishing phylogenies between fishes and tetrapods, not the least since these bones are prominent among determinable fossil finds of vertebrates.



TEXT-FIG. 1. View of the alternative homologizations and terminologies for the medial exocranial roof bones of osteolepiforms and stegocephalians. The upper row shows alternative terminologies in osteolepiforms, represented by *Eusthenopteron fords* (from Bjerring 1979, fig. 5). The lower row shows alternative terminologies in stegocephalians. Under A and D the reptilomorph *Paleoherpeton decorum* (from Panchen 1970, fig. 1)



Säve Söderbergh's interpretation

Westoll's interpretation

represents tetrapods generally. Under c the batrachomorph *Benthosaurus sushkini* (from Bystrow 1935, fig. 12) represents tetrapods generally. This latter form is used here since Säve-Söderbergh (1936) used batrachomorphs to demonstrate his interpretations. Under B, *P. decorum* and *B. sushkini* represent each other's respective group of tetrapods.

3. Obviously this dispute is also unfortunate since different terminologies make communication between scientists more difficult.

THE ARGUMENTS

Arguments for the orthodox interpretation. The main basis for the orthodox terminology of the early authors was seemingly the similarities in the positional interrelationships of the various dermal bones, and of dermal bones and other cranial structures. The sensory canals were apparently considered to be especially important in the latter context (e.g. Watson 1926a, p. 196, fig. 2; Goodrich 1958, pp. 284, 309).

Jarvik (1967, p. 186) claimed that 'the dermal bones as a whole are anchored to the part of the skull to which they belong'. He thus rejected the possibility of any movement of dermal bones relative to the endocranium. He also (p. 82) stated that frontals and parietals were defined by Gaupp (1905) as dermal bones covering respectively the orbitotemporal region with the adjoining part of the ethmoidal region, and the otic region, and he recently (Jarvik 1980b, p. 101) followed this up with definitions of these bones based on their relative positions to the tecta of the endocranial roof.

Jarvik (1967, p. 194, figs. 8, 9) compared the Devonian osteolepiform *Eusthenopteron foordi* with living anurans, and found extensive correspondences in positions of dermal bones relative to the endocranium. On the basis of these correspondences and of the definitions outlined above, and since the dermal bone homologies between anurans, reptiles, and mammals have never been doubted, the orthodox homologies and terminology for the bones in osteolepiforms were considered by Jarvik to be correct. This was also supported by direct comparisons of *Eusthenopteron* with a reptile and a mammal (Jarvik 1967, fig. 9).

When comparing osteolepiforms with primitive amphibians, Jarvik (1967) used Säve-Söderbergh's (1935, p. 198) division of the latter into Reptilomorpha and Batrachomorpha. When comparing osteolepiforms with reptilomorphs Jarvik (1967, p. 197) pointed out close correspondences in position between the spiracular slit of crossopterygians and the otic notch with its anterior continuation as seen in reptilomorphs. Jarvik thus claimed that the orthodox terminology showed the correct homologies in reptilomorphs. The interparietal position of the pineal foramen in this group was considered to be due to a change in the configuration of the brain (Jarvik 1967, p. 199, fig. 13). However, for batrachomorphs, Jarvik (1967, p. 201, fig. 11) considered that a deviation from the orthodox terminology was necessary.

In *Ichthyostega*, correspondences in dermal bone and sensory line patterns, and in relative positions of dermal bones and endocranial regions, with that of osteolepiforms, made Jarvik (1967, p. 201) consider it necessary to change the terminologies used by Säve-Söderbergh (1932) and himself (Jarvik 1952). An additional argument was the presence in *Ichthyostega* of a claimed rudiment of the intracranial joint, situated beneath the suture between the bones previously called parietals and postparietals (Jarvik 1952) and parieto-frontals and parieto-extrascapulars (Säve-Söderbergh 1932).

On the basis of correspondences in relative positions of dermal bones and structures of the palatoquadratum and endocranium, between osteolepiforms and *Ichthyostega* on the one hand, and between osteolepiforms and batrachomorphs other than *Ichthyostega* on the other, Jarvik (1967, p. 203) considered that the terminology proposed for *Ichthyostega* was also valid for other temnospondyls.

Arguments for Säve-Söderbergh's interpretation. As evidence for the presumed fused components in the dermal bones, Säve-Söderbergh (1932, p. 96, fig. 19) illustrated a specimen of *Eusthenopteron foordi* in which the parietals were divided into anterior and posterior components. The position of the borders between the components fused into the dermal bones were based on positions of sutures between adjacent dermal bones (Säve-Söderbergh 1932, p. 90). He also claimed support (1932, p. 94) from similarities in cheek plate and anterior part of the skull roof.

Arguments for Westoll's interpretation. Westoll's alternative (text-fig. 1D) was based on comparisons between osteolepiforms and stegocephalians, which were claimed to show a relative shortening of the

otico-occipital part of the endocranium at the transition from fish to tetrapods (Romer 1937, p. 52; 1941, p. 156; Westoll 1943, p. 83, fig. 3). This observation, together with assumed needs to have the same dermal bones situated above the otico-occipital part of the endocranium (e.g. Westoll 1943, pp. 81, 83, fig. 3), and to have the pineal foramen situated between homologous bones in osteolepiforms and stegocephalians (e.g. Romer 1937, p. 51), led to the assumption that the dermal bones that covered the relative short otico-occipital region in stegocephalians, had gone through a relative shortening at the transition from fishes to tetrapods that corresponded to the shortening of the otico-occipital region. On the assumption that the postparietals (or dermo-supraoccipitals) are homologous among tetrapods generally (e.g. Westoll 1961, p. 608), as was also stated in the orthodox terminology, Westoll's terminology (text-fig. 1D) seemed probable. A claimed lack of postparietals, or the presence of small such bones, in reptiles, was considered to be an end result of this trend of reduction (Romer 1937, p. 52; 1941, p. 159).

The cranial shield of the Devonian form *Elpistostege* (Westoll 1938) was considered as supporting evidence for the posterior transfer of dermal bones. This was found to fit between osteolepiforms and *Ichthyostega* in an evolutionary series from osteolepiforms to stegocephalians and also pelycosaurs (e.g. Westoll 1943, fig. 4). Westoll (1943, p. 81) also used as an argument the mode of formation of large bones, which he claimed had taken place in the frontal and nasal regions of dipnoans (*Fleurantia*), and which thus, he claimed, could also have taken place in crossopterygians. He thus considered the problem arising from his scheme as solved, which of the dermal bones in the osteolepiform skull roof, the nasals and frontals of tetrapods had developed from.

DISCUSSION OF THE ARGUMENTS

A discussion of homologies must be based on an unambiguous concept of homology. The only criterion that I find to be useful in a definition of such a concept is that of phylogenetic continuity or common ancestry. Criteria such as similar relative positions to other structures, common embryological origin, similar structure, etc., can merely be indications of varying importance. It is necessary to emphasize this since concepts referred to as homology are sometimes used in the literature, concepts in which phylogenetic continuity is considered to be of minor importance relative to, for example, relative position, common embryological origin, etc. It may also be useful to emphasize that when a name is given to a dermal bone, this name denotes a unity of bone tissues delimited from other dermal bones by sutures, and not, for example, a region of the whole dermal skeleton.

Since the assumption that there is a constant positional relationship between dermal bones and endocranial structures is basic to the arguments for all three alternatives that differ from the orthodox view, I will first discuss this assumption in some detail, and then successively discuss the other arguments of the main proponents of these alternatives.

Discussion of allegation of constant relative positions between dermal bones and endocranial structures. Jarvik (1952, p. 52, fig. 22; 1967, p. 194, figs. 8, 9) showed clearly that the parietals and frontals in certain reptiles and mammals covered approximately the same regions in the endocranium as the bones which in the orthodox terminology were called parietals and frontals in osteolepiforms. From the principle of constant positional relations between dermal bones and endocranial structures, since the 'type locality' of the names Parietal and Frontal is in man (Westoll 1961, p. 608; Jarvik 1967, p. 181; Patterson 1977, p. 83), and since the homologies of these bones are generally accepted from man to early reptiles, the terminology used by Jarvik for these bones in osteolepiforms must be correct.

However, what Jarvik has not taken into consideration is that it is not only in batrachomorphs that the bones called postparietals in orthodox terminology covered the otic region of the endocranium, but that also, according to reconstructions by Watson (1926a, figs. 12, 13, 15) and by Panchen (1970, figs. 1, 2), this feature is present in the reptilomorph *Paleoherpeton* (= *Paleogyrinus*) (text-fig. 2C). *Paleoherpeton* is an anthracosaur, here used as defined by Säve-Söderbergh (1934, p. 9; 1935, pp. 12, 104) and used by, for example, Panchen (1970, p. 1). The exocranial bone pattern of *Paleoherpeton* is

fairly typical for anthracosaurs (Panchen 1970, fig. 11). If following the allegation discussed here, the terminology generally used in this group must also be changed accordingly. For example, should the posteriormost exocranial pair of bones be called parietals, not postparietals. Anthracosaurs have been considered a suitable link between reptiles and rhipidists (e.g. Romer 1967, fig. 1; Panchen 1970, p. 1), and the main difference between the exocranial bone patterns of anthracosaurs and a cotylosaur like *Captorhinus* is that the supratemporal and intertemporal have disappeared as separate bones in *Captorhinus* (text-fig. 2A, c). If the allegation discussed here is followed, we thus get the situation that in two groups, which are considered comparatively close to each other in phylogeny, and which have very similar exocranial bone patterns, corresponding bones in these patterns should have different names. This must be considered a discrepancy.

The same type of discrepancy is even more distinct if comparing anthracosaurs with seymouriamorphs. The latter are often grouped with anthracosaurs (e.g. Säve-Söderbergh 1932, p. 202; Romer 1966, p. 363; Panchen 1975, p. 609; 1980, pp. 343–344). The exocranial bone patterns of, for example, *Seymouria* and *Paleoherpeton* are virtually identical (text-fig. 2B, c), the differences being restricted to the relative lengths of nasals and lacrymals, a posteriorly longer cheek plate in *Paleoherpeton*, and the shapes of some bones. However, the positional relationship between the medial exocranial bones and endocranial structures in the two forms are different (text-fig. 2B, c). Thus also here, the result of the principle of constant positional relations between dermal bones and endocranial structures is that corresponding bones in nearly identical exocranial patterns in supposed phylogenetically close forms should have different names.

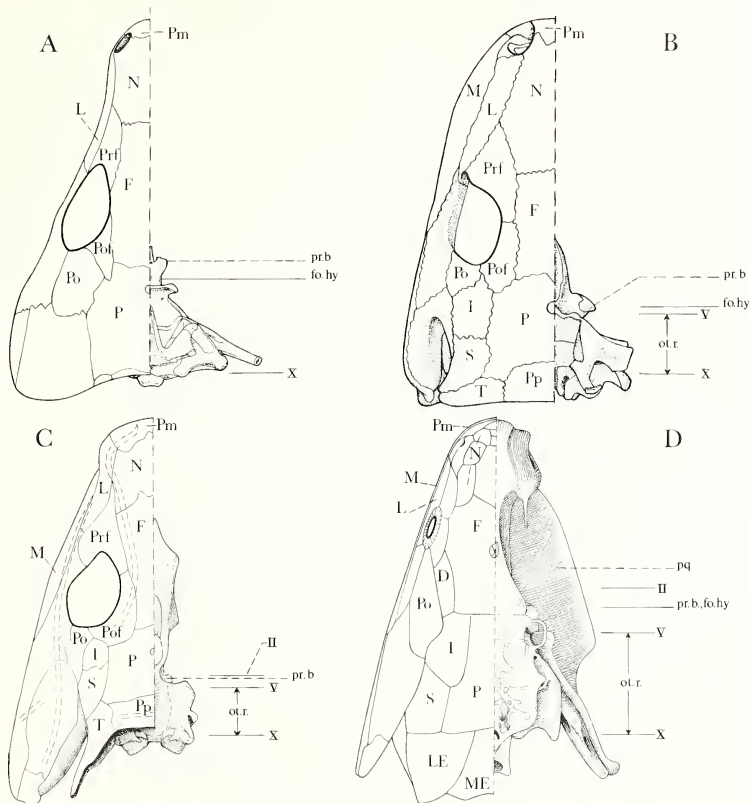
From the above reasoning it is clear that Jarvik's way of using the allegation discussed here leads to discrepancies.

In Westoll's and Romer's use of the postulate of constant relative positions between dermal bones and endocranial structures there are also discrepancies. Both these authors did not consider the clear fact emphasized by Jarvik (1967), that in mammals the otic region is often covered by the parietals, and thus if the allegation discussed here is valid, the terminology for the osteolepiforms must be as stated in the orthodox terminology. However, although they disregard this alleged constancy in this sense, they did use it when they claimed that the relative shortening of the endocranium in the evolution from fish to tetrapods was connected with a reduction of the bones they called postparietals. Westoll and Romer thus sometimes disregard and sometimes use this allegation. Their reasoning is also somewhat strange when the absence of the postparietals in some reptiles is considered to be the end result of this trend. If the connection between endocranium and dermal bones is assumed strong enough to deduce a reduction of the latter because of a relative reduction of the former, the lack of postparietals in some tetrapods (e.g. Romer 1941, p. 159) should mean that the otical part of the endocranium should be missing in these forms. Since this part is not missing in these forms, this reasoning of Westoll and Romer is illogical.

The above discussion shows that the uses by proponents of both main alternatives, i.e. those of Jarvik and Westoll, of an alleged constancy in position between dermal bones and endocranial structures, lead to discrepancies. A possible existence of such a constancy can also be discussed in more general terms. It may be examined by (1) studying how in ontogeny the relative position between dermal bones and endocranial parts are determined, and (2) by comparing the relative positions between dermal bones and endocranial structures in forms where the dermal bone homologies are generally accepted.

The crucial problem with respect to point (1) is whether there are any interdependencies between the ontogenetic processes determining the positions of dermal bones and those determining the positions of endocranial structures. If any such interdependencies exist and are unchangeable during phylogeny, an absolute constancy in relative positions can be said to exist between dermal bones and endocranial structures, but only then. However, if these interdependencies can be changed during phylogeny, e.g. as an adjustment to what is functionally beneficial, an absolute constancy cannot exist.

Two types of interdependencies between dermal bones and chondrocranial structures can be



TEXT-FIG. 2. Crania of A, a cotylosaur (*Captorhinus*, based on Romer 1956, fig. 36A; and Price 1935, pls. 6, 7); B, a seymouriamorph (*Seymouria*, based on White 1939, fig. 1, pl. 1B); C, a reptiliomorph (*Paleohierpeton*, based on Panchen 1970, figs. 1, 2); D, an osteolepiform (*Eusthenopteron*, based on Bjerring 1979, fig. 5; Jarvik 1954, figs. 1, 24). The left side of the crania shows the exocranial bones, and the right side the endocranium. Interrupted lines point to certain cranial structures, whole lines mark the antero-posterior level of cranial structures. Abbreviations are explained on p. 752.

considered. 1. The genetic process directing the ontogenetic development of a specific dermal bone is dependent on the presence of specific chondrocranial structures, or tissues that develops into such structures. 2. There is a functional interdependency where, for example, a dermal bone is dependent on some chondrocranial structure to be able to fulfil its function.

With respect to the first point, it seems doubtful that there is an inductive dependency between

chondrocranium and dermal bones. Moss (1968, p. 366) claimed that dermal bone ossification is the result of a series of inductive interactions between the basal layer of the epidermal cells and the ectomesenchym in the dermis. In contrast, the experimental works of Schowing (1968*a*, *b*, *c*) and Benoit and Schowing (1970) indicate that some cranial roof bones of birds were formed through induction by parts of the brain. Frontals were the results of induction by prosencephalon and mesencephalon, parietals were formed through induction by rhombencephalon and mesencephalon, and occipitals through induction by rhombencephalon. Hall (1978, p. 51) stated that similar results had also been obtained in forms other than birds, e.g. tests with regeneration of dermal bones in dogs had shown that this was dependent on induction by dura mater. Schowing (1968*a*, p. 51) also mentioned the possible importance of dura mater. According to Hall (1978, p. 51), the results of Schowing and Benoit indicate some sort of site specificity of the interactions between brain and dermal tissues. However, this site specificity can seemingly be determined not only by the brain, since if it was, the 180° turn of the developing brain (Benoit and Schowing 1970, fig. 23) should have led to the development of complete frontals, etc., in the neck. One or more still unknown factors must probably therefore also be effective. An experimental work of relevance in this context is also that of Leibel (1976) who studied the relationship in ontogenetic development between the otic capsule and dermal bones, and stated (p. 88) 'a parietal plate of normal proportions invariably forms in the complete absence of an otic capsule'.

With regard to the second point, functional interdependencies between endocranial parts and dermal bones apparently may exist. Lebedkina (1968, p. 318) demonstrated that the premaxilla receives support from the ethmoidal part of the endocranium in some holosteans and brachiopterygians. Such relationships are also indicated by Leibel (1976, pp. 89, 95) who stated that 'fine adjustments of parietal bone morphology, however, seem to depend in large part on the neighboring otic capsule, particularly the extent of posterior spreading of the otic process and planar orientation of the entire parietal base', and 'the otic capsule apparently functions as a substrate or surface for the condensation of osteo- and chondrogenic mesenchym'. However, such interdependencies appear to be changeable through phylogeny. This was demonstrated in the work by Lebedkina (1968). She showed that the support for the premaxilla by chondrocranial structures in the larva of some fishes did not exist in the larvae of urodeles. In the latter, this function had been taken over by the dermal bones posterior to the premaxilla.

As a conclusion to the above discussion of how relative positions between dermal bones and endocranial structures are determined in ontogeny, it can be stated that nothing indicates a mechanism leading to a constant positional relationship between parts of the skeleton.

The variation in relative positions between cranial roof bones and endocranial structures can be studied also by comparing them in forms in which the dermal bone homologies are evident and generally accepted. The best endocranial structures for such comparisons would have been the tecta which constitute the endocranial roof, and on which Jarvik (1980*b*, p. 100) based his definition of the exocranial roof bones. However, these tecta are often missing as complete mineralized structures in amniotes where the homologies are generally accepted (Goodrich 1958, p. 246, figs. 263, 264, 274, 275, 281), and are thus difficult to study in fossil material. This makes them inconvenient for such comparisons. Because of this, and also because structures like the otic capsules and the fossa hypophyseos were used in the arguments for the different homology alternatives (Säve-Söderbergh 1936, p. 145; Romer 1941, p. 158; Westoll 1943, p. 83, figs. 3-4; Jarvik 1967, pp. 194, 196), comparisons based on these latter structures are also of interest, and they have been used here.

Interesting comparisons can be made, for example, between *Bos* and *Equus* (Ellenberger-Baum 1943, figs. 830, 831). The frontal-parietal suture is situated far more posteriorly in *Bos* than in *Equus*. In *Equus*, like in man, the parietals constitute the cranial roof above the otic capsules, while in *Bos* they make part of the nuchal and lateral surfaces of the brain case. The hypophysis is situated beneath the anterior part of the parietals in *Equus*, and the middle part of the frontals in *Bos*. *Equus* is thus not so different from man in these respects, while *Bos* is. This difference is probably due to an adaptation to the presence of horns in *Bos*. In another mammal, *Ornithorhynchus* (Jollie 1962, figs. 3-8), the fossa hypophyseos is situated beneath the middle or posterior part of the parietals,

and in a baleen whale the cranial roof is mainly made of maxillaries and supraoccipitals (e.g. Slijper 1962, fig. 34).

The above descriptions of relative positions between dermal bones and endocranial structures show that they are variable. However, this variation can be interpreted as variation around a specific positional interrelationship that seem to be fairly common, and in which the postparietals cover the occipital region, the parietals cover the otic region, the frontals the orbitotemporal region, and the nasals the main part of the ethmoidal region. The seemingly frequent occurrence of this pattern may possibly be the reason for the notion that there is a fixed positional relationship between certain dermal bones and endocranial structures. However, this apparent stable positional relationship probably merely reflects the constancy of structures when there is no selective pressure working for changes. Put in other words, the parietals usually cover the otic region because they usually constitute the main posterior part of the exocranial roof, and the otic region constitutes the main posterior part of the endocranium. Changes in this configuration occur when there is a selective pressure for changes. I discuss evidence below to suggest that the disagreement regarding the homologies of the exocranial roof bones of crossopterygians and tetrapods is due to different misunderstandings of a deviation from this seemingly common positional relationship. However, before this, I will briefly discuss some other arguments used by the proponents of the different alternatives.

Discussion of additional arguments for Westoll's alternative. Westoll's use (1943, p. 81) of the possible fusion of bones in dipnoans is a weak argument. That bones may fuse during phylogeny is now, I believe, generally accepted (e.g. Patterson 1977, p. 92). It is thus evident that the osteolepiform nasals and postrostrals may have fused into both the nasals and frontals of tetrapods. However, the interesting point is whether the former bones fused into both these latter pairs of bones or only one pair. To the solution of this problem, this reasoning of Westoll contributes little.

The restricted value of the pineal foramen has been pointed out by Jarvik (1967, p. 185) and by Parrington (1967, p. 233).

The value of the exocranial bone patterns of *Elpistostege* and *Ichthyostega* has probably also been somewhat exaggerated. The patterns in these two forms seem to me a rather weak basis for stating general trends in the evolution of the vertebrate cranial roof. At the transitional stage from water to land, it is easy to imagine that a great deal of variation occurred.

Discussion of additional arguments for Jarvik's alternative. Jarvik's (1967, p. 197) homologization of the spiracular slit in osteolepiforms with the anterior continuation of the otic notch in reptilomorphs seems reasonable. However, Panchen (1970, p. 9) considered the otic notch of antracosaurs as homologous with the spiracular slit of osteolepiforms, and the anterior continuation of the otic notch, which Panchen called 'kinetic edge', as homologous with a presumed postero-lateral continuation of the transverse intracranial joint connecting this joint with the spiracular slit. Since this interpretation of Panchen's is possible and not disproved, Jarvik's argument is not conclusive. Since, however, the spiracular is a much more distinct opening than the assumed connection between the transverse joint and the spiracular, the transfer of the latter into the anterior continuation of the otic notch is a larger change than transferring the spiracular slit into this structure. On this basis the interpretation of Jarvik seems most probable.

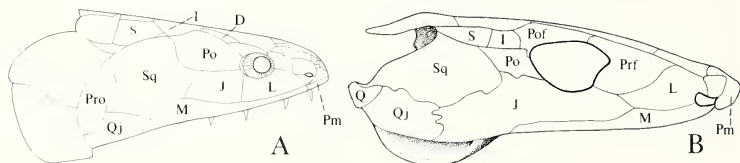
Jarvik's interpretation (1952, fig. 35b; 1967, p. 203; 1980a, p. 241) of the postero-medial bone in *Ichthyostega* as a parieto-extratemporal seems sensible on the basis of the position of the bone and the presence and course of the occipital transverse sensory canal. The position of the claimed rudiment of the intracranial joint in *Ichthyostega* may also be important, but the conclusion reached from its position is again based on the assumed constant positional relationship between dermal bones and endoskeleton. Jarvik's transfer of the terminology of *Ichthyostega* to other batrachomorphs is based solely on this assumption, and is thus questionable.

Discussion of arguments for Säve-Söderbergh's alternative. Säve-Söderbergh's (1932, p. 90) reconstructions of components of compound exocranial bones on the basis of sutures between neighbouring bones seem questionable to me. Dermal bones often change positional interrelations,

and differences may even exist between left and right sides of the same individual, e.g. as in *Acipenser* (Jarvik 1948, p. 68, figs. 18, 19). The specimen of *Eusthenopteron foordi* referred to (Säve-Söderbergh 1932, fig. 19, p. 96) indicates that the parietals are compound bones. However, neither this nor claimed similarities in the dermal bone patterns of the cheek plate and the snout between ichthyostegid and crossopterygians (1932, p. 94), make the reconstructions of the components in the compound dermal bones more reliable.

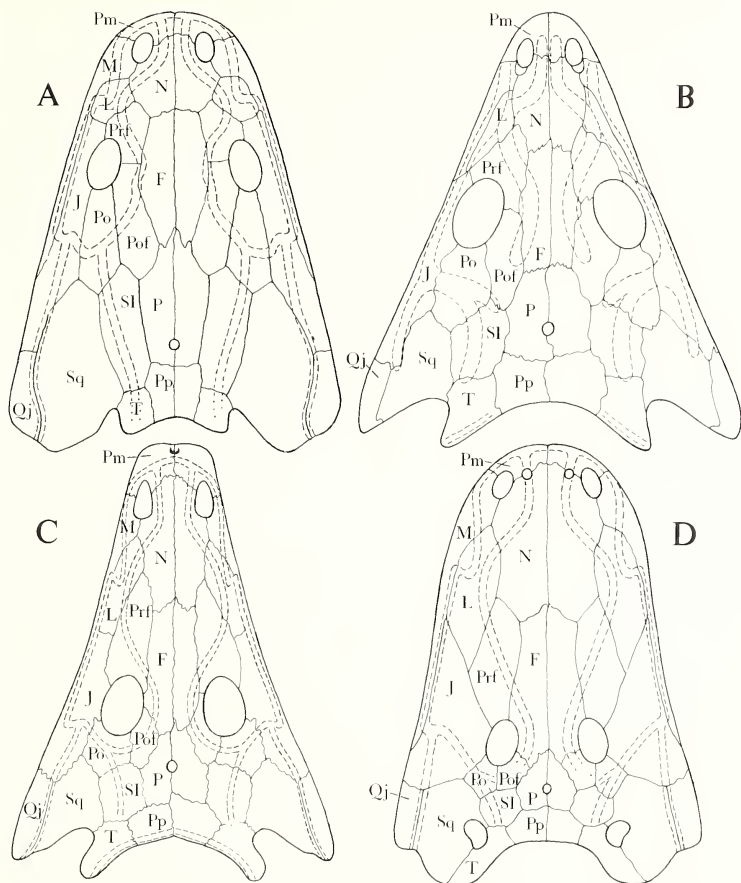
THE PROBABLE SOLUTION

Since in my view the basic criterion for homology is that of evolutionary continuity, it is necessary to study the exocranial roof bones in the transitional groups between osteolepiforms, in which the correct homologies and thus terminology is disputed, and reptiles in which the terminology used is generally accepted as correct. These transitional groups are presumably included in the assemblage of early amphibians denoted as stegocephalians. As mentioned above, these were divided by Säve-Söderbergh (1935) into reptilomorphs and batrachomorphs. I will in this article use this division as a basis for comparisons even if the correctness of Säve-Söderbergh's system may be disputed. I do so because this division is basal to Jarvik's (1967) interpretation, and also since major assemblages equivalent to those of Säve-Söderbergh are present also in other taxonomic systems for the stegocephalians, e.g. in that of Romer (1966). The more detailed systematics of the stegocephalians are probably not important to the conclusions drawn from the comparisons below.



TEXT-FIG. 3. Crania of A, an osteolepiform (*Eusthenopteron*, based on Bjerring 1979, fig. 1), and B, a reptilomorph (*Paleoherpeton*, based on Panchen 1970, fig. 1B), viewed from the right side, and showing antero-posterior lengthening of the dermal cheek bones at the transition from the former to the latter group. Abbreviations are explained on p. 752.

Comparisons with reptilomorphs. In comparing the Carboniferous anthracosaur *Paleoherpeton* with the Devonian osteolepiform *Eusthenopteron* it can be seen that their exocranial bone patterns are very similar (text-figs. 1, 2, 3). The main changes necessary to transfer the bone pattern of *Eusthenopteron* into that of *Paleoherpeton* include (1) a transfer of the nasals and postorbitals of the former into the nasals of the latter, (2) a relative increase of the orbital fenestra, and (3) the possibly most important in this context, a lengthening and flattening of the exocranium. As noted previously by several authors (e.g. Romer 1966, p. 80; Jarvik 1967, p. 188), a cranial lengthening is distinct in the preotical region of the cranium at the transition from osteolepiforms to stegocephalians. In the exocranium of *Paleoherpeton* this is shown clearly in the relatively increased length of the frontals, the anterior sutures of which become situated anterior to the orbital fenestrae. Also apparently the parietals have been slightly expanded anteriorly, having their anterior sutures situated anteriorly to the intertemporals. *Paleoherpeton* also has the jaw articulation situated more posteriorly relative to the neurocranium than *Eusthenopteron* (text-fig. 2). This is the result of an antero-posterior expansion of the cheek plate which, like the expansion of the frontals and parietals, is presumably connected with a general antero-posterior stretching of the dermal cranium. The stretching of the cheek plate is also shown in the lengthening of squamosum, jugal, and quadrato-jugal (text-fig. 3). Other changes at the transition from *Eusthenopteron* to *Paleoherpeton* include the disappearance of the operculars, which



TEXT-FIG. 4. Exocrania of four batrachomorphs placed in a succession of increasing snout lengths showing that this increase largely coincides with an increase in anterior extensions of the medial exocranial bones. A, *Buettneria* (based on Bystrow 1935, fig. 22); B, *Lyrocephalus* (based on Säve-Söderbergh 1937, fig. 3); C, *Benthosaurus* (based on Bystrow 1935, fig. 12); D, *Cyclotosaurus* (based on Bystrow 1935, fig. 23). Abbreviations are explained on p. 752.

leaves space for the otic notch, and that the lateral extrascapulars, or part of them, have possibly fused with the post-temporal and in this way become tabulars with tabular horns. Whether the medial extrascapular divides directly into the paired postparietals is unclear, but because of this uncertainty, and to promote terminological simplicity, I prefer to call these bones in tetrapods postparietals and not, for example, left and right medial extrascapulars. The reason why the extrascapulars of osteolepiforms, when becoming anthracosaur postparietals, moved from their supraoccipital position in the former group to the supraorbital position in the latter (text-fig. 2c) can only be guessed at. A plausible explanation is that the anterior movement of the more anterior dermal bones made it necessary for the posteriormost dermal bones to follow this movement. This may be combined with a need to free the neck region of dermal bones to allow independent movement of the head.

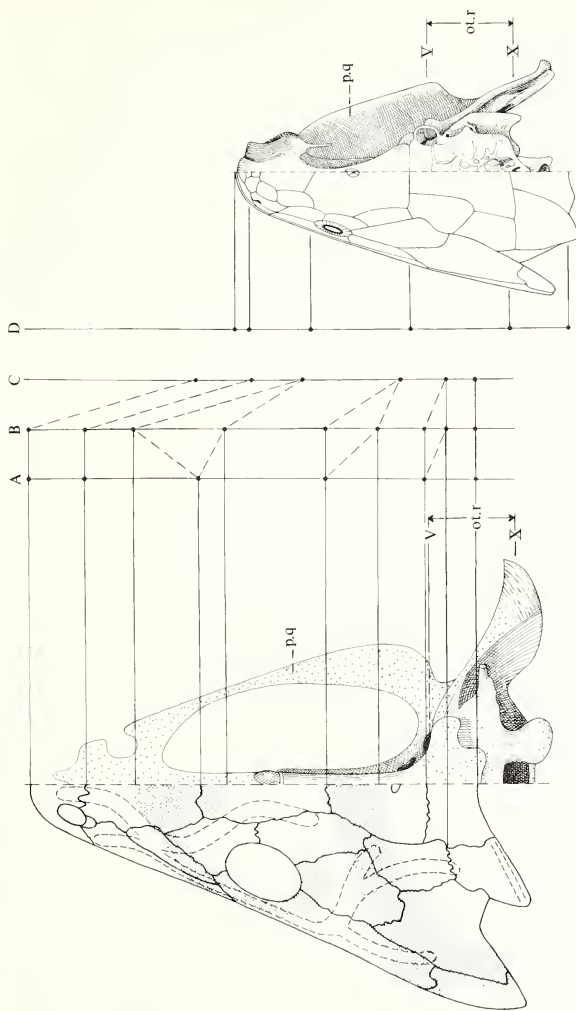
From the comparisons above, it is clear that relatively few changes are necessary to change the exocranial bone pattern of osteolepiforms to that of anthracosaurs. Assuming that the generally accepted homologizations between reptiles and anthracosaurs are correct (text-fig. 2A, C), the necessary result becomes that the homologies and terminologies used for osteolepiforms in the orthodox terminology and as used by Jarvik (text-figs. 1A, B) are correct. This is also consistent with the most probable interpretation of what is homologous with the osteolepiform spiracular slit in the exocranial roof of anthracosaurs (see above).

Comparisons with batrachomorpha. Säve-Söderbergh (1935, p. 202) included in Batrachomorpha the groups Ichthyostegalia, Labyrinthodontia, Phyllospondyli, and possibly Pantyloidei and Anura. The two latter groups are not important for this study. Since the dermal bone pattern of labyrinthodonts seemingly shows relatively little variation (text-fig. 4; e.g. Säve-Söderbergh 1935, 1936), and because this pattern is similar to that of primitive phyllospondyls (Watson 1921, p. 73), it is sufficient to compare with a limited number of forms.

Comparisons between an osteolepiform like *Eusthenopteron* and a labyrinthodont like, for example, *Lyrocephalus* (text-fig. 5) indicate that similar processes to those that took place at the transition from osteolepiforms to anthracosaurs also occurred at the transition from osteolepiforms to labyrinthodonts. This implies that the terminology for the five medial exocranial bones in batrachomorphs is the same as in reptilomorphs and most other tetrapods (text-fig. 4). This is in agreement with the orthodox terminology, but in conflict with the terminologies of Säve-Söderbergh and Jarvik. The following arguments support this assumption.

The above-mentioned relative lengthening of the preorbital cranial region at the transition from the osteolepiforms to stegocephalians was in labyrinthodonts, as in anthracosaurs, connected with an anterior transfer of the sutures between the dermal bones along the midline. Indications of this connection are seen when comparing short- and long-snouted stegocephalians with *Eusthenopteron*. In short-snouted forms such as, for example, *Buettneria*, *Lyrocephalus* (text-fig. 4), and *Eusthenopteron* (text-fig. 2) the frontals stretch only slightly anterior to the orbits, while in long-snouted forms like *Benthosaurus* and *Cyclotosaurus* (text-fig. 4C, D) the frontals usually stretch distinctly anteriorly to the orbits. This anterior shift of the anterior suture of the frontals is usually followed by the frontal-parietal suture. This is shown by their anterior position relative to the laterally situated presumed supra-intertemporals. In a similar way, although less distinct, the postparietals protrude anteriorly to the tabulars.

Indications of anterior shifts in positions of the exocranial bones along the midline are also shown by Bystrow (1935) and Säve-Söderbergh (1937). They demonstrated distinct growth zones in the surface sculpture of the cranial roof bones. Even if the growth indicated by these zones shows ontogenetic growth, it must also indicate a phylogenetic change from adult stages of *Eusthenopteron* to adult stages of more or less long-snouted labyrinthodonts. In this connection it is interesting to note that if the lengths of the medial exocranial bones in a labyrinthodont were to be reduced with the lengths of the growth zones (stages A-B, text-fig. 5), and thereafter these reduced bones were placed in the natural succession from the posterior end forwards (stages B-C, text-fig. 5), the sutures between these reduced frontals and nasals, and between frontals and parietals, would be approximately level with the corresponding sutures in a cranium of *Eusthenopteron* where the otic region (ot.r., text-fig. 5)



TEXT-FIG. 5. Illustration of relative differences in antero-posterior extensions of exocranial bones and endoskeletal features of a labyrinthodont (*Lyrocephalus auri*, from Sæve-Søderbergh 1936, fig. 14; 1937, fig. 3), and an osteolepiform (*Eusthenopteron foordi*, from Jarvik 1954, figs. 1, 24; Bjerring 1979, fig. 1). The crania are figured with equally long otical regions. Their left sides show the exocrania, and the right sides the endoskeleton. On the exocranium of *Lyrocephalus* are the growth zones marked by shading. The antero-posterior extension of the medial exocranial bones of *Lyrocephalus* are projected on to stage A. In stage B these lengths, minus the lengths of the respective growth zones, are shown. The transfer of this reduction is marked by interrupted lines. In stage C the lengths set out in stage B have been placed adjacent to each other, in natural succession from the level of the posterior margin of the postparietals of *Lyrocephalus*. The transfer of bone positions that change in this step is marked by interrupted lines. In stage D is projected the antero-posterior extensions of the medial exocranial bones of the cranium of *Eusthenopteron*. Abbreviations are explained on p. 752.

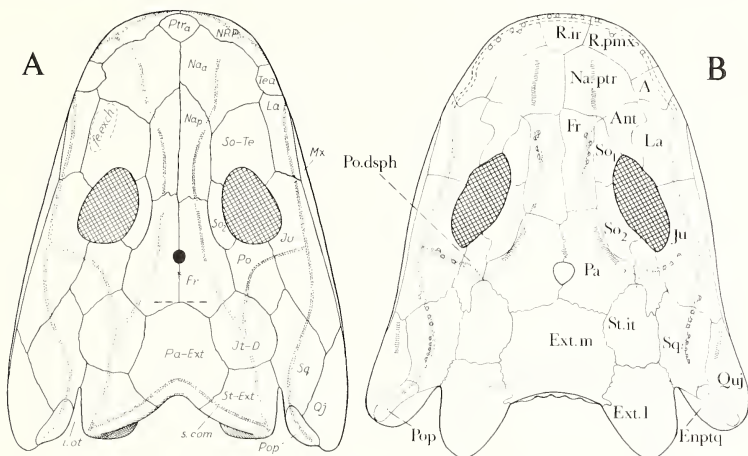
is of the same length as in the labyrinthodont (stages C–D, text-fig. 5). This result necessitates a growth zone also in the postparietals. No growth zones have been claimed in this bone by Säve-Söderbergh (1937), but Bystrow (1935, table p. 24) indicated a slight growth. A lack of distinct traces of growth zones on the postparietals may be explained by the gradual transformation of the surface sculpture from oblong grooves to rounded pits (Bystrow 1935, p. 84, fig. 11g–h; Säve-Söderbergh 1937, p. 197, figs. 7, 8). It should also be pointed out that the anterior pits on the postparietals often are distinctly more oblong than the posterior pits (Bystrow 1935, figs. 12, 15, 27; Säve-Söderbergh 1937, figs. 1, 4A, 5, 10A). An anterior expansion of the postparietals is indicated also by the posterior position in these bones of the transverse occipital canal, and from the succession of ontogenetic stages in *Sclerophagus* and *Archegosaurus* shown by Romer (1939, figs. 2, 3). It is thus clear that the sutures between probably all the medial exocranial bones was transferred more or less anteriorly at the transition from osteolepiforms to labyrinthodonts in connection with a lengthening of the cranium. The corresponding endocranial lengthening is, as shown by comparing otical and preotical proportions of the endocranium and palatoquadrate of osteolepiforms and labyrinthodonts (text-fig. 5), mainly restricted to the preotical part. The necessary result of this general lengthening of the medial dermal bones and limited lengthening of the endocranium is that the postparietals in labyrinthodonts occupy a position covering the otic region of the endocranium. The fact that the hind margin of the postparietals is concave in labyrinthodonts and straight or convex in osteolepiforms indicates that this margin has moved forward at the transition from osteolepiforms to labyrinthodonts. These bones thus left the supraoccipital position they, as extrascapulars, had in osteolepiforms. The adaptive reason for this change probably was to allow the head to move independently of the body.

From the above reasoning it is clear how the exocranial bone pattern of osteolepiforms probably developed into that of labyrinthodonts, and that the five exocranial bones along the midline in labyrinthodonts are the same five that are situated along the midline in the reptilomorph exocranium. The exocranial terminology for the batrachomorphs following from this is shown in text-fig. 4.

The only batrachomorph that possibly makes an exception to the above-stated terminology for the five medial exocranial bones, is the Devonian *Ichthyostega*. The transition from osteolepiforms to *Ichthyostega* presents the problem of whether the postero-medial exocranial bone in the latter is a medial extrascapular which has expanded anteriorly as suggested by Jarvik (1952, fig. 35). This would make the bones along the midline the same five as in other stegocephalians, and may also be considered supported by similarities in the dermal bone patterns of *Ichthyostega* and other batrachomorphs (text-figs. 4, 6). If the parietals in certain labyrinthodonts like, for example, *Lyrocephalus* (text-fig. 5), *Peltosaurus*, *Capitosaurus*, *Heptasaurus*, *Wetlugasaurus* (Säve-Söderbergh 1935, figs. 26, 36A, 37, 38) were to move forward somewhat, they would occupy a position very similar to the paired dermal bones which in *Ichthyostega* surrounds the pineal foramen. The anteriorly protruding part of the postero-medial bone may be due to an anterior expansion corresponding to the anterior expansion of the postparietals of many labyrinthodonts (text-fig. 4). However, if so, this anterior expansion has gone very far in *Ichthyostega*, and the fact that such large anterior expansions mainly are found in long-snouted labyrinthodonts, while *Ichthyostega* is short snouted, speaks against this interpretation.

The alternative solution, that the postero-medial bone in *Ichthyostega* results from a fusion between the parietals and the medial extrascapular, was suggested by Säve-Söderbergh (1932, p. 78, figs. 2, 4) and Jarvik (1967, p. 203, fig. 11c). However, these authors differed in their views in that Säve-Söderbergh considered that only the posterior part of the parietals had fused with the medial extrascapular, while Jarvik considered that the whole parietal did so. Säve-Söderbergh's alternative is unlikely because it would mean both that the parietals in *Ichthyostega* are unusually large, and that they are positioned unusually far anteriorly. As already mentioned, the latter is unlikely in a short-snouted form like *Ichthyostega*. Jarvik's alternative (text-fig. 6A) is supported by the following similarities between the posterior interorbital bone in *Ichthyostega*, which in Jarvik's scheme must be the frontals, and the frontals in *Eusthenopteron*. 1. These bones in the two forms have the approximate same position relative to the orbital fenestra, the bones in *Ichthyostega* being situated

slightly more posteriorly. 2. If the frontals and dermosphenotics in *Eusthenopteron* fuse, the result are bones which in shape and position are nearly identical to the bones in *Ichthyostega*. 3. In both forms these bones surround the pineal foramen. 4. The supraorbital sensory canal runs through both the discussed bones in *Ichthyostega*, and the frontals in *Eusthenopteron*, while the postero-medial exocranial bone in *Ichthyostega* and the parietals in *Eusthenopteron* lack sensory canals. 5. The



TEXT-FIG. 6. Exocrania of *Ichthyostega* showing respectively A, Jarvik's (1967, fig. 11c) interpretation of dermal bone and sensory canal pattern, and B, Säve-Söderbergh's (1932, fig. 15) interpretation of the same. Abbreviations: A, anterior antorbital; Ant., posterior antorbital; Enptq., quadrate ramus of entopterygoid; Ext.l., lateral extrascapular; Ext.m., parietoextrascapular; fe.exch., fenestra exchoanal; Fr., frontals; i.ot., otic notch; It-D., intertemporo-dermosphenotic; Ju., jugal; La., lachrymal; Mx., maxillary; Na., anterior nasal; Na., posterior nasal; Na.ptr., naso-postrostral; NRP., naso-rostro-premaxillary; Pa., parietal; Pa-Ext., parieto-extrascapular; Po., postorbital; Po.dsph., postorbito-dermosphenotic; Pop., preopercular; Ptra., anterior median postrostral; Qj. and Quj., quadratojugal; R.ir., rostro-interrostral; R.pmx., rostropremaxillary; So., anterior supraorbital; So., posterior supraorbital; So-Te., supraorbito-ectal; Sq., squamosal; St-Ext., supratemporo-extrascapular; St.it., supra-temporo-intertemporal; Te.a., anterior tectal.

claimed rudiment of the intracranial joint in *Ichthyostega* is also a possible support for this alternative. The significance of these correspondences between the bones in *Ichthyostega* and *Eusthenopteron* is indicated by the presumed primitiveness of *Ichthyostega*. On the basis of the arguments discussed above, Jarvik's alternative (text-fig. 6A) seems to me the most probable.

The bones antero-lateral to the parieto-extrascapulars were called supratemporo-intertemporals by Säve-Söderbergh (1932; text-fig. 6B), and intertemporo-dermosphenotics by Jarvik (1967; text-fig. 6A). The postero-lateral bones were thus called lateral extrascapulars and supratemporo-extrascapulars, respectively. While Jarvik thus considered the dermosphenotic to be fused with the intertemporals, Säve-Söderbergh considered it to be fused with the postorbital. In a later study, Jarvik (1980a, p. 241) mentioned the possibility of a fusion between dermosphenotics and frontals. These alternatives may be judged from the viewpoints of relative positions to the surrounding dermal bones, the sensory canals, and the otic notch.

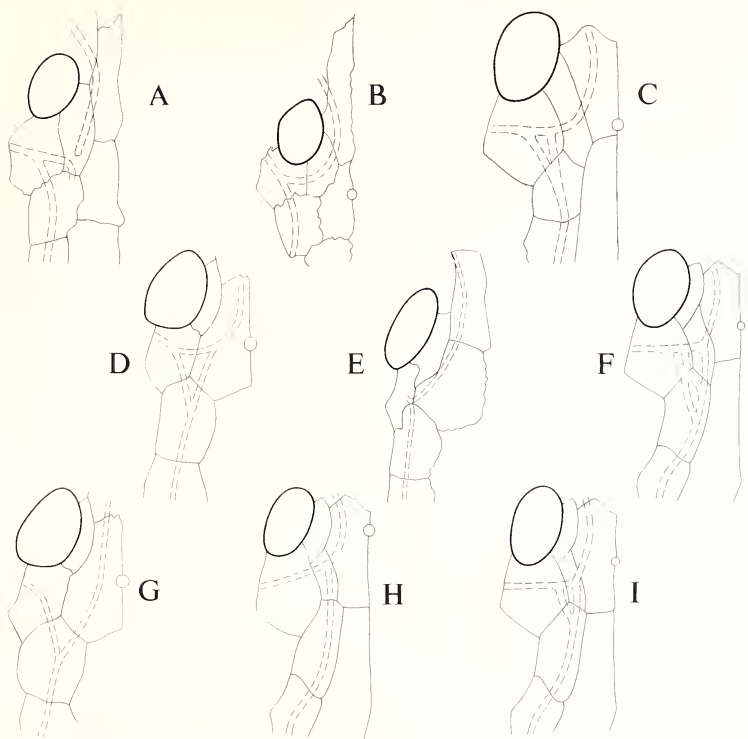
The dermosphenotics in *Eusthenopteron* are situated between the postorbitals and the posterior parts of the frontals, and borders anteriorly on the posterior supraorbital (text-fig. 2D). Together with the fact that a fusion in *Eusthenopteron* between frontals and dermosphenotics would lead to bones very similar both in shape and position to the presumed frontals in *Ichthyostega* (text-fig. 6A), this indicates that this bone in *Ichthyostega* is a fronto-dermosphenotic. A possible counter-argument to this is the position of the junction between infraorbital and supraorbital canals, which in *Eusthenopteron* is situated in the dermosphenotics. This was presumably the basis for the interpretations of both Säve-Söderbergh and Jarvik, since they interpreted the course of the sensory canals, which are very indistinct in the known specimens, differently (text-fig. 6). However, both these interpretations of the position of this junction may fit the presence of a fronto-dermosphenotic bone. This is due to an apparent transfer of this sensory canal junction from the dermosphenoticum to the postorbitals, in the transition from osteolepiforms to the labyrinthodonts. This makes the position of this junction a weak argument in determining bone homologies in this region and in these forms. That this change in position of this junction occurred is indicated by: (1) that the dermal bone containing this junction in labyrinthodonts is, judging from its position relative to both the orbit and the surrounding dermal bones, clearly a postorbital; and (2) that several stegocephalians have sensory canal patterns that may be interpreted as intermediate stages in such a transition. Examples of such forms are *Trematosaurus* (Bystrow 1935, figs. 18D, 25), *Lyrocephalus* (Säve-Söderbergh 1935, figs. 61, 66), and *Aphaneramma* (Säve-Söderbergh 1935, fig. 56; 1936, fig. 31).

Theoretically there are several ways in which this change may have taken place, and it is interesting to note that both Säve-Söderbergh's and Jarvik's interpretation of the position of the junction in *Ichthyostega* may fit as an intermediate stage in some theoretical succession. If the junction gradually moved from the dermosphenoticum to the postorbital (text-fig. 7H $\rightarrow$ E $\rightarrow$ B) Säve-Söderbergh's interpretation of the position of the junction would fit as an intermediate stage between osteolepiforms and labyrinthodonts. Another alternative is that a connection developed directly between postorbital and intertemporal (text-fig. 7H $\rightarrow$ D). Examples of specimens approximately at this stage are given by Bystrow (1935, fig. 18A, C). From this stage there may either be a reduction of the postorbital-dermosphenotic connection, or a reduction of the dermosphenotic-intertemporal connection. The first leads to a sensory canal pattern like Jarvik's interpretation of *Ichthyostega* (text-figs. 6A, 7G), the latter to the pattern that is common in labyrinthodonts (text-fig. 7B). A possible intermediate in the latter process is shown in a specimen of *Lyrocephalus* (text-fig. 7A). A third alternative is that a series of branchings took place, which gradually 'moved' the junction on to the postorbital (text-fig. 7H $\rightarrow$ I $\rightarrow$ F $\rightarrow$ C $\rightarrow$ B). The presence of branched sensory canals in this region is shown by Bystrow (1935, p. 115, figs. 18B, D, 25).

To solve the problem of which way the position of the junction changed, a more detailed study, and probably more material, is needed. However, the existence of so many specimens with branching canals makes the first of the three alternatives, that the junction gradually 'wandered' to its new position, somewhat less probable. This again can theoretically be considered to reduce somewhat the probability for Säve-Söderbergh's interpretation of the position of the junction in *Ichthyostega*. No matter how this change took place, however, the reasonings above leave no doubt that the change in position occurred, and thus that there are no valid arguments against the existence of a fronto-dermosphenotic. This also supports Jarvik's interpretation concerning which bones are frontals and parietals in *Ichthyostega* (text-fig. 6A).

A very tentative interpretation of the phylogenetic position of *Ichthyostega* based on the estimated bone homologies, and also partly on the above theoretical discussions on the sensory canal patterns, is that it is in several aspects a primitive tetrapod belonging to a side-branch from a line between osteolepiforms and other stegocephalians.

Two other forms possibly on the tetrapod side of the osteolepiform-tetrapod transition, that should be mentioned briefly, are the Devonian *Elpistostege* and *Acanthostege*. To my knowledge *Elpistostege* is known only from a single specimen (Westoll 1938, fig. 1), showing only some of the medial exocranial bones. It seems similar to *Ichthyostega*, but too little is known to warrant any further discussion. *Acanthostege* is also a relatively little known form (Jarvik 1952, p. 68; 1980a, p.



TEXT-FIG. 7. Sketches of temporal regions of exocrania showing possible transitional stages of the junction of infraorbital and supraorbital sensory canals between that of osteolepiforms (H) and a common labyrinthodont pattern (B). A, *Lyrocephalus euri* (from Säve-Söderbergh 1937, fig. 1); B, *Benthosaurus sushkini*, (from Bystrow 1935, fig. 12); C, D, theoretical intermediate stages; E, *Ichthyostega* (from Säve-Söderbergh 1932, fig. 15); F, theoretical intermediate stage; G, *Ichthyostega* (from Jarvik 1967, fig. 11c); H, *Osteolepis* (from Jarvik 1967, fig. 11A); I, theoretical intermediate stage. The orbit is marked by a thick line.

242), and thus does not allow any thorough analysis of homologies or relationships. The exocranial sutures of the specimens of *Acanthostega* are very indistinct, but granting that Jarvik's interpretations of these are correct, I find his reasonings well founded. To his statements I will only add that, in its position relative to the squamosum, and to the skull table generally, the process positioned posteriorly on the skull roof is very similar to the tabular process of the anthracosaurs.

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ABBREVIATIONS

The following abbreviations are used in all text-figures except text-fig. 6: D, dermosphenotic; F, frontal; fo.hy., fossa hypophyseos; I, intertemporal; J, jugal; L, lachrymal; LE, lateral extrascapular; M, maxillary; ME, medial extrascapular; N, nasal; ot.r., otic region; P, parietal; Pm., premaxillary; Po., postorbital; Pof., postfrontal; pq, palatoquadratum; Pp, postparietal; pr.b., processus basiptyergoideus; Prf., prefrontal; Pro., preopercular; Q, quadratum; Qj., quadratojugal; S, supratemporal; SI, supra-intertemporal; Sq, squamosum; T, tabular; II, nervus opticus; V, nervus trigeminus; X, nervus vagus.

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ENTOMOZOACEAN OSTRACODS FROM THE LOWER CARBONIFEROUS OF SOUTH-WESTERN ENGLAND

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ABSTRACT. The Entomozoacea ('entomozoids') are an important group of Palaeozoic ostracods which flourished in the upper Devonian and lower Carboniferous. Although they have traditionally been regarded as planktonic, the carapace morphology of the entomozoaceans provides no clear evidence for either a planktonic or benthic existence and it is concluded that both these modes of life may have been represented within the group. This paper is the first significant published account of these ostracods in the British Carboniferous. Sixteen species from the Tournaisian of Devon, south-western England, are described and illustrated. Six are assigned to known species, one (*Maternella (M.) whitewayensis* sp. nov.) is new and the remainder are dealt with under open nomenclature. The British assemblages, particularly those from excavations made near Whiteway Barton, closely resemble faunas from the lower and middle *latior* Zone of entomozoacean chronology (broadly equivalent to the *Gattendorfia ammonoid* Stufe) reported by Groos-Uffenorde (1974) from the Rheinische Schiefergebirge.

THE ostracods described in this paper belong to the families Entomozoidae Přibyl, 1949 and Rhomboentomozoidae Gründel, 1962 which are regarded herein as constituting the superfamily Entomozoacea Přibyl, 1949. The entomozoaceans (often called 'entomozoids')—a term avoided here because it is ambiguous—are a peculiar Palaeozoic group in which the carapace is weakly calcified and usually bears a characteristic ribbed ornamentation, giving rise to their colloquial name 'finger-print ostracods'. They are often considered to have been planktonic and have long been known to occur abundantly in upper Devonian deep-water slates, particularly in Germany where they have proved to be of considerable stratigraphic value (Rabien 1954, 1956). It has become apparent more recently that entomozoaceans are also important in lower Carboniferous (Tournaisian and Viséan) rocks of similar facies (Bless 1973; Becker and Bless 1974; Gründel 1962; Tschigova 1970, 1975; Sanchez de Posada 1977; Groos-Uffenorde in press). Species have been described, or at least illustrated, from the lower Carboniferous of Germany (Kummerow 1939; Rabien 1960; Gründel 1961, 1963, 1979; Koch 1970; Groos-Uffenorde 1974, in press; Sanchez de Posada and Bless 1974), Spain (Jordan and Bless 1970), Poland (Błaszyk and Natusiewicz 1973), U.S.S.R. (Posner 1958; Tschigova 1977), China (Wang 1978), and Canada (Green 1963) as well as from the upper Carboniferous (Namurian A) of Spain (Becker 1975, 1976). However, apart from a few obscure species of '*Entomis*' (Jones 1873, p. 416) and three species which have been briefly mentioned recently (Selwood *et al.* 1982, table 1), no Carboniferous entomozoaceans have yet been documented in the British literature.

The main purpose of the present paper is to describe a small but important collection of these ostracods from the Tournaisian of Devon, south-western England. Much of the material was obtained during the remapping of I.G.S. 1:50,000 sheet 339 (Newton Abbot) under an Institute of Geological Sciences-Exeter University contract. It is all in the form of internal and external moulds in slates and shales and for the most part is well preserved. The literature on entomozoaceans is principally German, the major publication being the monograph of Rabien (1954), and they remain unfamiliar to many English-speaking ostracod specialists. In order to provide some introduction to the group, a brief, general account of the preservation, shell structure, and carapace morphology of upper Devonian and lower Carboniferous species is given here together with a consideration of their palaeoecology in the light of morphological features. A review of the stratigraphic distribution of Carboniferous entomozoaceans follows the systematic section.

PRESERVATION, SHELL STRUCTURE, AND CARAPACE
MORPHOLOGY OF THE ENTOMOZOACEA

Preservation. Unlike those of most fossil ostracods, entomozoacean shells very rarely survive as calcareous objects which can be extracted from the rock matrix. They occur most commonly as internal and external moulds in slates and shales (Rabien 1954, p. 21), the cavity between the moulds sometimes partly occupied by reddish-brown material, presumably some form of iron-oxide. In this mode of preservation the valves are almost always disarticulated (Rabien 1954, p. 14) and, as fully discussed by Rabien (1954, pp. 22–25), they are frequently subject to tectonic deformation. According to its orientation with respect to the tectonic 'stretching direction', a specimen may be extended or compressed parallel to its long axis or deformed obliquely into an asymmetric shape (Gooday 1973, fig. 3.5). Deformation can therefore modify taxonomic characters such as valve outline, length/height ratio, and rib spacing and must be taken into account when describing or identifying species.

Entomozoaceans are sometimes preserved in limestones, where they may occur as complete articulated carapaces (Rabien 1954, pp. 13–14). Several such specimens of *Entomozoe* (*Nehdentomis*) *nehdensis* Matern from upper Devonian limestones were examined in section and by scanning electron microscopy by Langer (1973, p. 25). Building on the preliminary observation of Rabien (1954, p. 14), Langer demonstrated that the shell was represented by a thin outer layer (3–5 μm thick) which formed the ornamentation, and an underlying crypto- or microcrystalline layer (15–25 μm thick). He believed that the crystalline structures observed were secondary, the original, weakly calcified shell having been completely replaced by calcite.

Other types of preservation have occasionally been reported. Silicified valves were obtained from limestones by Blumenstengel (1965) and Becker (1977) while Gooday (1973, p. 19) recorded the occurrence of articulated carapaces in the form of external moulds in decalcified 'gingerbread' nodules. Pyritized internal moulds are occasionally found in slates and limestones (Gooday 1973, p. 18; Lethiers 1974, p. 64).

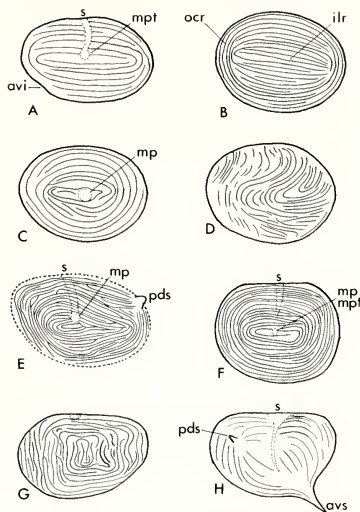
Shell structure. The entomozoacean carapace was probably weakly calcified like that of Recent members of the family Halocyprididae (Kummerow 1939, pp. 81, 85; Triebel 1941, p. 327; Rabien 1954, pp. 14, 17; Langer 1973, p. 25; Becker 1976, p. 215; 1977, p. 472). The ribs, however, may have been rather more strongly calcified than the rest of the shell. Langer (1973, p. 25) speculated that, as in recent myodocopids (a group which includes the halocypridids), the carapace wall contained embedded particles of amorphous calcium carbonate as well as oil droplets to aid buoyancy. The shell also seems to have been thin ('sehr dünnchalige': Rabien 1954, p. 14; Becker 1976, p. 216) although Langer (1973, p. 25) believed that this was not true in the case of *E. (N.) nehdensis*. Entomozoacean valves are occasionally dislocated in a manner suggesting that they were torn prior to preservation (text-fig. 3; Gooday 1973, p. 20; see also Triebel 1941, p. 327). These observations clearly support the notion of a thin and rather flimsy shell. According to Becker (1977, p. 472) there was also an internal chitinous layer which was 'very thick and . . . formed the interior sculpture'. This seems to echo Groos-Uffenorde's (1974, pp. 78–79) suggestion that the two different types of rib present on external moulds of *Maternella schindewolfi* (Kummerow) were derived from different shell layers.

A rather different view of the nature of the carapace wall was put forward by Blumenstengel (1965, 1973). He argued that because valves may sometimes be silicified, they must have originally been heavily calcified, the calcite having been replaced by silica. This opinion was strongly challenged by Becker (1977, p. 472). However, Becker (1976, p. 216) himself drew attention to a rare species of *Entomoprimitia* from the Frasnian of Belgium which undoubtedly possessed a thick, heavily calcified shell.

Carapace morphology. Carapace terminology is summarized in text-figs. 1 and 2.

Many entomozoaceans apparently have valves of equal size (Rabien 1954, p. 14) although Langer (1973, p. 25) found that in *E. (N.) nehdensis*, the right valve projects beyond the left valve along the dorsal margin. There is no evidence for any kind of hinge structure and the valves were therefore

TEXT-FIG. 1. Carapace outlines and rib patterns of typical upper Devonian and Carboniferous entomozoaceans. A-E, family Entomozoidae, subfamily Entomozoinae; F, G, subfamily Entomoprimitiinae; H, family Rhomboentomozoidae. A, generalized *Entomozoe* (*Nehdentomis*). B, generalized *Richterina* (*Richterina*). C, *Maternella* (*Maternella*) *dichotoma* Paeckelman (based on Rabien 1954, pl. 1, figs. 8, 9). D, *Kuzminaella venusta* Tschigova (based on Tschigova 1977, pl. xiii, fig. 6). E, *Truyulsina tuyulsina* Becker (based on Becker 1976, text-fig. 3). F, *Entomoprimitia* (*Entomoprimitia*) *kayseri* Waldschmidt (based on Rabien 1954, pl. 2, fig. 13). G, *Bertilionella* (*Rabienella*) *kegeli* (Matern) (based on Rabien and Rabitz 1958, text-fig. 5). H, *Ungerella* cf. *mempeli* Kummerow (based on Groos-Uffenorde 1974, text-figs. 7, 12). Abbreviations: avi, antero-ventral indentation of margin; avs, antero-ventral spine; ilr, inner longitudinal rib; mp, muscle patch; mpt, muscle pit; ocr, outer concentric rib; pds, postero-dorsal spine; s, sulcus. Except for *Ungerella*, the anterior end points left. Drawn at various scales.

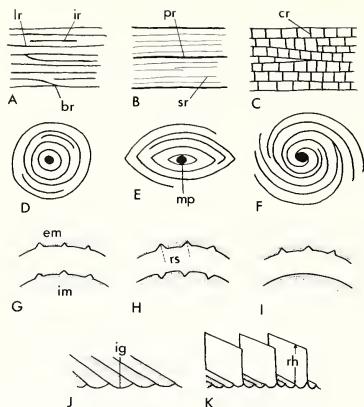


presumably joined in life by an organic, or perhaps chitinous membrane as in the halocypridids. To explain the disarticulated occurrence of valves in deep-water slates, it must be assumed that any such connecting structure decayed rather rapidly after death. Eye tubercles are not developed (Triebl 1941, p. 330; Becker 1976, p. 216). Sexual dimorphism of the carapace has not been reliably documented.

The lateral outline varies considerably within the superfamily but rounded, circular to more or less oval shapes tend to predominate (text-fig. 1). The family Rhomboentomozoidae is characterized by a triangular to subrectangular outline in which the dorsal margin is long and straight; members of the family Entomozoidae, subfamily Entomoprimitiinae are asymmetrically oval and have a shorter straight dorsal margin, while in the subfamily Entomozoinae, the outline is more or less oval with a curved dorsal margin. A slight antero-ventral concavity of the margin is present in some species of *Maternella*, *Entomozoe*, and *Entomoprimitia* (Rabien 1954, p. 94; Gooday 1973, pp. 60-61).

The rhomboentomozoids have a single prominent sulcus (also called a nuchal furrow) arising from near the middle of the dorsal margin and curving downwards so that the concave side faces anteriorly. A sulcus is strongly developed, weakly developed, or absent in most members of the Entomozoidae. However, the subfamily Bouciinae, a poorly known Silurian group which is atypical of the entomozoaceans on a whole, has two sulci, one originating from the dorsal and one from the ventral margin. Two variably developed carapace swellings are present in certain species of the subgenus *E.* (*Entomoprimitia*), the larger one situated antero-ventrally with a smaller inflation behind the sulcus. Antero-ventral and postero-dorsal spines arise from the valve surface in *Ungerella* while *Rhomboentomozoe* bears a single ventral spine and *Truyulsina* has a postero-dorsal spine. Terminal spines are developed at the ends of the valves in two species of *R.* (*Richterina*).

The area of adductor muscle attachment is expressed on the surface of the valve by a pit or a smooth, oval, or circular patch. The pit is either a ventral expansion of the sulcus or an isolated depression. Numerous tiny, circular muscle scars were observed to occur within the muscle pit of *Richterina* (*Fossirichterina*) *semen* (Jones) by Gooday (1973, p. 107). The subgenus *Richterina*



TEXT-FIG. 2. A-K, ribbing terminology. A, longitudinal ribs (lr) with short, intercalated ribs (ir) and bifurcating ribs (br). B, longitudinal ribs differentiated into primary ribs (pr) and secondary ribs (sr). C, longitudinal ribs joined by cross-ribs (cr). D, circular concentric ribs. E, lenticular, concentric ribs. F, spiral ribs around central muscle patch (mp). G, internal mould (im) and external mould (em) with similar ornamentation and H, with reversed ornamentation (rs, rib spacing). I, ornamented external mould with smooth internal mould. J, normal ribs separated by intercostal grooves (ig). K, flange-like ribs (rh, rib height), each pair separated by two normal ribs.

(*Volgina*) has a characteristic small, elongate depression near the dorsal margin of each valve. This may be homologous with the dorsal muscle scar area of some other ostracods (Rabien 1954, p. 15) within which originate muscles connected to various limbs and body parts (Andersson 1974, fig. 10).

In almost all upper Devonian and Carboniferous entomozoaceans the exterior surface of the valve bears ribs separated by intercostal grooves (text-figs. 1 and 2). These are often of uniform strength but in some species are differentiated into stronger primary and weaker secondary ribs. Short cross-ribs may be developed and these subdivide the intercostal grooves into rows of pits. Occasionally, for example in *Bertillonella* (*Rabienella*) *cicatricosa* (Matern), the ribs are replaced by a series of spines arranged in rows. Ribs which extend out from the valve surface as wide flanges have recently been documented (Gooday 1973, p. 61; Becker 1977, p. 469). These structures, referred to herein as 'flange-like ribs' are known to occur in the genera *Richterina*, *Maternella*, and *Ungerella*.

Entomozoacean ribs usually follow a more or less regular course, their arrangement and spacing being characteristic for particular species. Elongate carapaces, such as those of *Richterina* and *Entomozoe*, tend to have basically longitudinal ribbing, although in most cases a variable number of outer ribs run concentrically, parallel to the valve margin. In forms with a more rounded outline, the ribs are arranged in a spiral or concentric pattern around a central point (usually the muscle patch) and parallel to the margin. This kind of pattern is found in *Entomoprimitia*, *Truyulsina*, and particularly *Maternella*. Some species have, in addition, a number of more longitudinal, free ending inner ribs. A basically spiral or concentric type of ornamentation is also developed in *Bertillonella*, although here the ribs often follow a somewhat irregular, subtriangular, or subquadrate course. The recently described genus *Kuzminaella* has an unusually irregular, swirling pattern of ribs.

The ornamentation of the original inner surface of the valve, as recorded by internal moulds, usually consists either of ribs or grooves corresponding to the ribs on the outer surface (text-fig. 2G-I). However, the inner surface is occasionally smooth and does not reflect the external ornament.

PALAEOECOLOGY OF THE ENTOMOZOACEA

It has been suggested that entomozoaceans, traditionally regarded as planktonic organisms, were in fact wholly, or in part benthic. In this section these alternative modes of life are scrutinized in the light of certain aspects of the functional morphology and ecology of some Recent ostracods.

Entomozoaceans as planktonic ostracods. Following Kummerow (1939, pp. 80–81), most authors have maintained that entomozoaceans were probably members of the open ocean plankton or micronekton (Triebl 1941, p. 327; Gründel 1962, p. 1196; Becker 1976, p. 215). The morphological evidence includes: (i) the thin, weakly calcified, often streamlined carapace, (ii) the convex ventral margin, and (iii) the tendency for the carapace to become rounded with a high surface–volume ratio (Triebl 1941, p. 327; Gründel 1962, p. 1196; 1965, pp. 599, 606; Becker 1976, p. 215). In addition, the recently documented flange-like ribs of some species increase the surface area of the shell and hence would have retarded its sinking velocity, an obvious advantage for a planktonic animal. The world-wide distribution of entomozoaceans, together with their abundance in facies which are often virtually devoid of other fossils (Franke and Paul 1980, p. 238), also argues for a planktonic existence (Becker 1976, p. 215).

Particular ecological parallels have been drawn between entomozoaceans and the Halocyprididae, a group which includes most of the living, truly oceanic planktonic ostracods. Halocypridids generally occur throughout the water column, but are most abundant at depths of between 100 and 300 m. They are powerful swimmers, propelling their light, generally weakly calcified, boat-like carapaces through the water with surprising speed 'in a zig-zag series of darts' (Lochhead 1968, p. 456) by means of the exopodites of the second antennae. These structures, which bear long swimming setae, emerge through the rostral incisure and strike outwards, backwards, and slightly downwards in a motion resembling the breast stroke (Skogsberg 1920, p. 119; Iles 1961, pp. 304, 323). This powerful swimming stroke is facilitated by the presence of a horizontally orientated rostral incisure and a hollowing of the carapace surface behind the incisure, features which allow a free backwards swing of the exopodite. The swimming musculature is contained in the very large triangular basal segment (protopodite) of the second antenna. The posterior margin of the protopodite is indicated on the carapace surface by a sulcus and, in some species, this segment is accommodated in an antero-dorsal 'shoulder vault' (Müller 1906, p. 6).

Triebl (1941, pp. 327–328), Rabien (1954, p. 15), and Becker (1976, p. 216) have argued that entomozoaceans also possessed a strongly developed second antenna protopodite because they often have a similar sulcus and, in a few species, an antero-ventral swelling which is comparable to the halocypridid shoulder vault. From the supposed presence of a large protopodite, it is inferred that they were sufficiently adept swimmers to maintain themselves in the plankton. However, it seems unlikely that the entomozoaceans swam like halocypridids because they have no rostral incisure. Rabien (1954, p. 94) has proposed that the swimming exopodites ('Ruder-Antennae') may have emerged at the antero-ventral marginal indentation which is present in a few species (see above). If this were the case, these species, at least, must have swum at best rather weakly since the swimming stroke would have included a significant downward component tending to rotate the carapace rather than drive it swiftly and horizontally forwards.

On the other hand, the absence of an incisure does not necessarily preclude a planktonic mode of life. In *Thaumatoecypris echinata* Müller, a very rare ostracod which has been caught only twice, this structure is absent. *T. echinata* is nevertheless planktonic (Kornicker and Sohn 1976b, p. 21) and apparently swims with downward and backward movements of the first and second antenna endopodites and exopodites (Skogsberg 1920, p. 119; Iles 1961, p. 322). It is also significant that *Polycopse*, which resembles many entomozoaceans in having an approximately circular outline and no rostral incisure, has a 'comparatively swift and rather tenacious method of swimming involving the first antennae, second antennae exopodites as well as the maxillae' (Skogsberg 1920, p. 119 footnote). However, members of this genus spend most of their time on the bottom and are not truly planktonic.

Entomozoaceans as benthic ostracods. This alternative hypothesis was first proposed by Blumenstengel (1965, 1973) because he believed that the entomozoacean carapace was more strongly calcified than had hitherto been suspected (see above). Kozur (1972a, pp. 642–643) also thought that entomozoaceans were benthic. He considered them to be typical, deep-water psychrosphaeric ostracods, mainly because they are absent, or very rare in upper Devonian cephalopod limestones. In

Kozur's view, the weakly calcified carapace and the widespread distribution and faunal uniformity of entomozoaceans are characteristic of benthic psychrosphaeric ostracods, as well as free-swimming forms, while their greater than average size and high surface to volume ratio he believed to be positive indicators of a deep-water, benthic existence. Becker (1977, p. 472), on the other hand, did not accept that entomozoaceans in general had heavily calcified carapaces and opposed the views of Blumenstengel and Kozur as being too far-reaching (Becker 1976, p. 216). However, he did accept (Becker 1976, p. 215) that the heavily calcified species of *Entomoprimitia* mentioned above was probably benthic.

There is no convincing morphological basis for rejecting the hypothesis that at least some entomozoaceans were benthic. In certain respects (weak calcification, lack of rostral incisure, rounded outline) genera such as *Bertillonella*, *Maternella*, and *Kuzminaella* resemble living representatives of the deep-sea family Thaumatoctyprididae which are mainly benthic or nekto-benthic (Kornicker and Sohn 1976b, p. 21). Like some of the Entomozoacea, many thaumatoctypridids possess an antero-ventral concavity of the margin (see particularly *Thaumatoconcha hessleri* Kornicker and Sohn 1976b, fig. 47). The concavity bears no obvious relationship to either the first or second antennae (Kornicker and Sohn, 1976b, p. 20), thus casting doubt on Rabien's (1954, p. 94) suggestion that the marginal indentation of entomozoaceans is a rudimentary rostral incisure.

Conclusion. No single conclusion regarding the palaeoecology of these ostracods can be derived from a consideration of their morphology. The evidence is ambiguous: the weak carapace calcification, flange-like ribs, and inferred presence of a large second antenna protopodite in some species all suggest a planktonic existence while the similarities between some entomozoaceans and the Recent, mainly bottom-dwelling thaumatoctypridids indicate that a benthic mode of life should not be ruled out for some species.

It is quite possible that a variety of ecologies are represented among upper Devonian and Carboniferous Entomozoacea. Some groups, perhaps those in which the sulcus and shoulder vault are weakly developed or absent, may have been benthic or nekto-benthic, like *Polycope* and most thaumatoctypridids. Rare, heavily calcified forms were almost certainly benthic (Becker 1976). Others may have been sufficiently strong swimmers to maintain themselves as permanent members of the plankton. Becker (1977, p. 472) also concluded that 'different modes of life are quite possible' for entomozoaceans. This view is supported by the fact that the halocypridids, sometimes regarded as ecological analogues of the entomozoaceans, are themselves not exclusively planktonic. Species of the important genus *Bathynochoecia* Decey are members of the deep-water benthos or, in the case of a species recently discovered in Bermuda, cavernicolous (Angel, pers. comm.).

MATERIAL

Geological Setting. In the area covered by the I.G.S. 1:50,000 Newton Abbot map, Devonian and Carboniferous rocks occupy six thrust-bounded successions which are characterized by distinct facies, particularly in the upper Devonian. The successions are summarized on Sheet 339 and in the Newton Abbot Memoir (in press). Lower Carboniferous entomozoids have been obtained from two of these sequences.

(i) The Teign Valley Succession. Entomozoaceans occur sparsely in the Hyner Shale, a formation comprising dark bluish-grey shales which span the Devonian-Carboniferous boundary, and also in the overlying grey and green shales of the Trusham Shale. This succession is structurally autochthonous and is characterized by an upright fold style.

(ii) The Ugbrooke-East Ogwell Succession. A well-preserved entomozoid fauna occurs in the Whiteway Slate. This formation consists of purple, grey and green slates and, like the Hyner Shale, it includes the Devonian-Carboniferous boundary. The Ugbrooke-East Ogwell Succession is allochthonous and characterized by recumbent, north-facing folds.

Full information on the structure and stratigraphy of the area will be published in the Newton Abbot Memoir.

Localities. The ostracods were obtained from the localities listed below. In the systematic section these are identified by abbreviations (WS1, etc.). The Newton Abbot Memoir includes an illustration (fig. 11) showing the position of the trenches and exposures at Whiteway Barton. Except where indicated, the specimens were collected by Drs. E. B. Selwood and R. A. Waters.

Whiteway Slate locality 1 (WS1): SX 88447525; exposure behind barn and cutting alongside it; north end of Whiteway Barton farmyard.

Whiteway Slate locality 2 (WS2): SX 88607545–88577754; loose debris collected from north-eastern side of ploughed field just north of Whiteway Barton.

Whiteway Slate locality 3 (WS3): SX 88577553; from trench trending 146° parallel to north-eastern edge of field between SW 88577533 and 88567555, beginning 24.6 m from north-western edge of field and running south-eastward for 30.4 m at distance of 3.6 m from north-eastern edge of field. Specimens collected from south-eastern end of trench to 5.2 m along it in north-westerly direction.

Whiteway Slate locality 4 (WS4): SX 88577553; specimens collected between 5.2 and 10.6 m from south-eastern end of same trench.

Whiteway Slate locality 5 (WS5): SX 88577554; specimens collected between 10.6 and 13.7 m from south-eastern end of same trench.

Trusham Shale locality 1 (TS1): SX 84268113; exposure on eastern side of track just north of Leigh Farm.

Trusham Shale locality 2 (TS2): SX 84288138; exposure produced by ploughing in field east and south of Emmett Copse.

Hyner Shale locality 1 (HS1): SX 84248123; exposure in same field, about 18.2 m south of locality TS2.

Bampton Limestone Formation locality 1 (BLF1): SS 97222385; exposure on western side of road, opposite Higher Hukely, north-east of Bampton. Collected by Dr. J. M. Thomas.

Techniques. Latex casts of external moulds were prepared according to the technique described by Rigby and Clark (1965). These casts precisely reproduce the external ornamentation of the shell and also produce better photographic results than the original specimens. All photographs were obtained on Kodak Panatomic × 35 mm film using the Leica Aristophot system with micro-mirror reflex attachment and bellows. The text-figures were drawn with the aid of a Wild M5 'Zeichentubus'.

SYSTEMATIC PALAEONTOLOGY

Following German practice, more than half of the sixteen species are described under open nomenclature (Matthews 1973). The suprageneric classification adopted in this paper is that of Gründel (1962, p. 1203). All specimens are deposited in the Institute of Geological Sciences in London (registration numbers AD2537–2551, 2676–2817) and Leeds (AD3686–3706, 3719–3759, ZO4386–4394).

Order MYODOCOPIDA Sars, 1866

Superfamily ENTOMOZOACEA Příbyl, 1949

Diagnosis. Large ostracods, usually > 1 mm, with weakly calcified carapace which lacks rostrum and rostral incisure. Sulcus well developed, weakly developed, or absent. Surface often with longitudinal, concentric, or spiral ribs. (Modified after Sylvester-Bradley 1961, p. 388).

Discussion. Following Gründel (1969, p. 30), this superfamily is limited to the families Entomozoidae and Rhomboentomozoidae. It is not considered to include the enigmatic Bolbozoidae. However, Gründel's (1969) combination of the Entomozoacea with the Entomoconchacea, another group of unusual Palaeozoic ostracods, to form the suborder Entomozocopina of the order Myodocopida has been refuted (Kozur 1972a, p. 7) and there is probably no close relationship between these two superfamilies. Indeed, Kornicker and Sohn (1976a) have argued that the Entomoconchacea probably belong to the Halocypridina (a suborder including the Thaumatoocypridacea and Halocypridacea) and may have been ancestral to the living thaumatoocypridaceans.

It has usually been considered that the Entomozoacea were related in some way to the myodocopids. Thus Sylvester-Bradley (1961, p. 388) placed them, with a question mark, in the suborder Myodocopina together with the extant superfamilies Thaumatoocypridacea, Cypridinacea, and Halocypridacea and the fossil Entomoconchacea. Polenova and Zanina (1960), however, classified the family Entomozoidae (= Entomozoacea) with the living Polycopidae (*Polyscope* and *Polycopsis*) in the suborder Cladocopa of the order Myodocopida. These two groups have in common the absence of a rostral incisure and, in some cases, an oval or circular lateral outline. The case for a

relationship between the entomozoaceans and polycopids has been argued by Kozur (1972a, p. 641; 1972b, p. 8). Analysis of evolutionary trends led him to the conclusion that an advanced entomozoacean, perhaps *Bertillonella*, was ancestral to the Carboniferous to Triassic genus *Discoidella*, which in turn evolved into *Polycope* and *Polycopsis*. Kozur (1972a, p. 641) found *Discoidella* very difficult to separate from polycopids in material from Triassic deep-water sediments. These opinions have been incorporated into two recent and authoritative classifications (Pokorný 1978, p. 130; Maddocks 1982, table 1) in both of which the entomozoaceans and polycopids are combined together within the suborder Cladocopa, order Myodopida.

The claim that polycopids are descended from entomozoaceans is difficult to assess because the classification of myodocopids is based largely on their soft-part anatomy (Kornicker and Sohn 1976b, pp. 4-6). However, several points argue against such a direct relationship. First, there is no immediately obvious similarity in the carapace shape of the two groups as there is between the Palaeozoic entomoconchaceans and their probable living descendants, the thaumatocypridaceans (Kornicker and Sohn 1976a, pls. 2, 3). The absence of a rostral incisure in both groups may be of no significance since this is a primitive condition and hence not evidence for a phylogenetic relationship (Kornicker and Sohn 1976b, p. 5). Secondly, some entomozoaceans have what appear to be thirty to fifty tiny, round adductor muscle scars (Gooday, 1973; 1978, pl. 1, fig. 9). There are only three such scars in polycopids. Thirdly, *Polycope* is known from the Carboniferous (Pokorný 1978, p. 132) and may occur as early as the middle Devonian (Whidborne 1890; Přibyl 1953), well before the first occurrence of *Discoidella*, or indeed *Bertillonella*. For these reasons I prefer at present to regard the Entomozoacea as a distinct Palaeozoic group of myodocopids of which the precise affinities are unclear (see also Kornicker and Sohn 1976b, p. 6).

Family ENTOMOZOIDAE Přibyl, 1949

Type genus. Entomozoe (Jones, 1861) *sensu* Přibyl, 1949.

Diagnosis. Valves of equal or slightly differing sizes. Lateral outline bean-shaped, egg-shaped, asymmetrically or symmetrically oval. Straight section of dorsal margin short, never corresponding to greatest carapace length and sometimes replaced by curved dorsal margin; dorsal angles rounded where present. Sulcus strongly developed, weakly developed, or absent; where present it is straight or concave towards anterior end. Secondly, postero-ventral sulcus developed in one subfamily (Bouciinae). Muscle attachment area either absent or represented by smooth patch or pit. Spines or protuberances occasionally developed. Ornamentation usually present and in most genera comprises ribs of equal or unequal strength. Ribs are arranged transversely (Bouciinae), longitudinally, spirally, or concentrically, but are occasionally irregular or broken into minute spines. (Slightly modified after Rabien 1954, p. 44; Gründel 1962, p. 1158.)

Discussion. The Entomozoidae comprises three subfamilies: the Entomozoinae, Entomoprimitiinae, and the Bouciinae, the latter including only the unusual Silurian genus *Boucia* Agnew.

Subfamily ENTOMOZOINAE Přibyl, 1949

Diagnosis. Lateral outline bean-shaped, egg-shaped, or symmetrically oval. Straight dorsal margin never clearly developed, sometimes absent. Ornamentation in earlier forms basically longitudinal with concentric ribs at end; in later forms concentric or spiral. (After Gründel 1962, p. 1203.)

Discussion. The Entomozoinae includes the following genera and subgenera: *Entomozoe* (Entomozoe) Přibyl, 1949; *E. (Richterina)* Jones, 1874; *E. (Nehdentomis)* Matern, 1929; *Kuzminaella* Tschigova, 1977; *Maternella* (Maternella) Rabien, 1954; *M. (Steinachella)* Gründel, 1979; *Rabienites* Tschigova, 1977; *Richterina* (Richterina) Gürich, 1896; *R. (Fossirichterina)* Matern, 1929; *R. (Volkina)* Rabien, 1954; *Truyulsina* Becker, 1975.

Genus RICHTERINA Gürich, 1896

Type species. *Cytherina costata* Rh. Richter, 1869.

Diagnosis. Lateral outline symmetrical, in form of elongate to broad oval with equally curved dorsal and ventral margins and equally rounded ends. Sulcus not developed. Central muscle pit or patch may be developed. Indentation of carapace near dorsal margin developed in one subgenus. Ornamentation comprises (i) longitudinal ribs of equal strength, inner ones ending free before ends of valve but outer ones continuing concentrically parallel to margin, or (ii) longitudinal primary ribs and weaker secondary ribs with cross-ribs sometimes also present. Terminal spines occasionally developed.

Subgenus RICHTERINA (RICHTERINA) Gürich, 1896

Diagnosis. Simple muscle pit not developed but muscle patch may be present. Dorsal indentation of carapace absent. Ribs typically of equal strength, inner ones ending free, outer ones running concentrically, but in one species of unequal strength. Terminal spines developed in two species.

Discussion. The difficulties created by Matern's (1929) designation of *R. (R.) costata* as the type species of *Richterina* are dealt with by Gründel (1962, p. 1201).

Richterina (Richterina) latior Rabien, 1960

Plate 74, fig. 1; text-figs. 3, 4A-F

(?) 1879 *Entomis gyrata* (Rh. Richter, 1856); Jones, p. 186, pl. xi, fig. 4.

(?) 1890 *Entomis richteri* Jones, pp. 321-322, pl. xi, fig. 3.

v* 1960 *Richterina (Richterina) latior* Rabien, pp. 69-74, pl. 1, figs. 1-4; pl. 2, figs. 6, 7.

v. 1961 *Richterina (Richterina) latior* Rabien; Gründel, pp. 123-125, pl. 11, fig. 6; text-figs. 13-16.

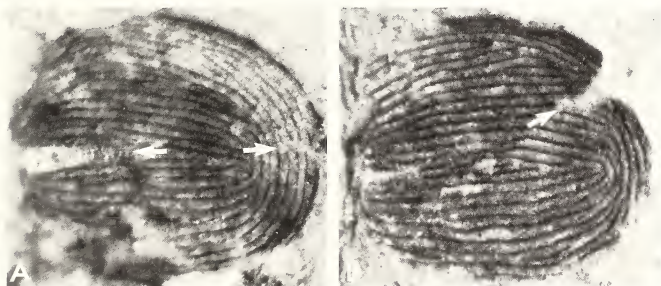
v. 1974 *Richterina (Richterina) latior* Rabien; Groos-Ufflenorde, pp. 80-81, pl. 4, fig. 5.

v. 1974 *Richterina (Richterina) latior* Rabien; Alberti, Groos-Ufflenorde, Streel, Ufflenorde and Walliser, p. 270.

(?) 1977 *Richterina (Richterina) latior* Rabien; Tschigova, pp. 105-107, pl. xiv, fig. 3.

(?) 1978 *Richterina (Richterina) latior* Rabien; Wang, p. 4, pl. 2, figs. 17, 18.

Diagnosis. Species of *Richterina* having broadly oval and symmetrical lateral outline with mean length/height ratio of 1.4-1.6. Surface bears twenty-five to thirty-five longitudinal ribs of equal



TEXT-FIG. 3. *Richterina (Richterina) latior* Rabien, 1960. Two external moulds photographed under glycerol. Note tear-like features (arrowed). A, AD2696, maximum dimension 1.70 mm. B, AD2696, maximum dimension 2 mm.

strength, following straight course with few bifurcations; at least four, usually six to twelve ribs are concentric at ends of valve, most of remainder terminate before ends. Rib spacing regular and relatively wide, averaging about 0.04 mm. Circular muscle patch interrupts several central ribs. (Modified after Rabien 1960, p. 69.)

Material studied. About ninety specimens: localities WS1 (AD2539, 2540, 2543, 2547, 2551); WS2 (AD2676, 2678, 2679, 2685–2688, 2691, 2692, 2692A, 2695, 2695B, 2696, 2697B, 2698A, 2698B); WS4 (AD2786); WS5 (AD2806); TS1 (AD3720, 3726, 3728, 3731, 3733, 3737, 3738, 3741); TS2 (AD3744, 3745, 3748, 3753–3756, 3758); HS1 (AD3686–3689, 3693, 3696, 3698–3670, 3702, 3704–3706).

Dimensions.

Adults

	Number of specimens	Range	Mean
Length (mm)	31	0.95–2.30	1.53
Height (mm)	31	0.60–1.75	1.05
L/H ratio	31	1.21–1.75	1.43

Juveniles

	Number of specimens	Range	Mean
Length (mm)	8	0.50–0.90	0.76
Height (mm)	8	0.40–0.70	0.57
L/H ratio	8	1.23–1.42	1.33

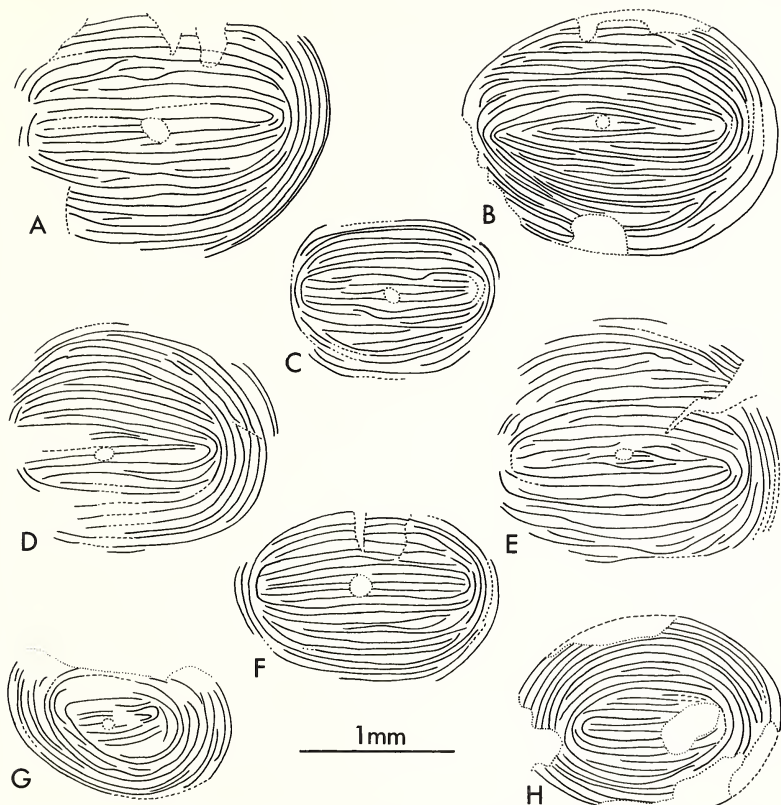
Description of British material

Adults. The lateral outline is broadly and symmetrically oval, with gently curved dorsal and ventral margins and broadly and equally rounded ends. The surface bears twenty-five to thirty-four narrow longitudinal ribs separated by broader intercostal grooves; five to eight outer ribs run concentrically, parallel to the ends of the valve. In one atypical specimen (text-fig. 4b) some of the ribs follow a rather more narrowly rounded course at one end of the valve. Ribs which are intercalated between the main ribs occur fairly frequently. The rib spacing varies from 0.032 to 0.070 mm (mean 0.045 mm) near the centre of the valve, decreasing slightly towards the margin. At the centre of most valves there is a smooth, circular, sometimes rather indistinct muscle patch, 0.075–0.15 mm in diameter, which cuts across one or two ribs.

Juveniles. The valves have a rather more elongate outline than the adults and bear twenty to twenty-seven ribs with a spacing of 0.023–0.032 mm.

Discussion. *R. (R.) latior* has been regarded as a typical richterinid which, according to Gründel (1962, pp. 1188–1190, fig. 5), evolved directly from *R. (R.) striatula* (Rh. Richter, 1848). Rabien (1960, p. 73) notes that these two species can be distinguished only by their length/height ratios, the number of concentric ribs and the rib spacing and remarks that between '*R. striatula* und der neuen Art bestehen also keine prinzipiellen, sondern nur graduelle Merkmalsunterschiede'. A closer scrutiny, however, reveals further differences. i. The adductor muscle attachment area is represented in *R. (R.) latior* by a circular patch which interrupts several ribs, but in *R. (R.) striatula* by a broadening of two adjacent intercostal grooves near the centre of the valve (Gooday 1978, pl. 1, fig. 3). Rabien (1960, p. 69) records an 'undeutlicher kleiner Fleck' near the centre of the valve, but a muscle patch is clearly visible in some of the British specimens. In view of the importance attached to the muscle attachment area in ostracod taxonomy, this difference between the two species may be of some significance. ii. Cross-ribs are sometimes present at the ends of the valve in *R. (R.) striatula* (Gooday 1978, pl. 1, figs. 2, 3) but are never developed in *R. (R.) latior*. iii. The ribbing pattern of *R. (R.) latior* is less regular, usually with more numerous intercalated ribs than in *R. (R.) striatula*, and always with some inner longitudinal ribs which curve around at the ends of the valve. iv. Internal moulds are clearly ornamented in *R. (R.) latior* but smooth in *R. (R.) striatula*. For these reasons it is concluded that the two species may not be particularly closely related.

It is interesting to note that the ribbing patterns of *R. (R.) latior* and *Maternella (M.) dichotoma* may be rather strikingly similar (compare particularly the somewhat unusual specimen illustrated in text-fig. 4b with Gooday, 1978, pl. 3, fig. 4). However, since the lateral outlines of these two species are



TEXT-FIG. 4. A-F, *Richterina* (*Richterina*) *latior* Rabien, 1960. A, AD2697B, internal mould. B, AD2698A, internal mould. C-F, AD2696, external moulds. G, H, *Richterina* (*Richterina*) sp. 1, internal moulds (G, AD2698B; H, AD2696).

different and conform clearly with the diagnosis of their respective genera (symmetrical in *R. (R.) latior*, asymmetrical in *M. (M.) dichotoma*), it seems likely that this resemblance is the result of convergent evolution.

Jones (1879, pl. xi, fig. 4) illustrated as *Entomis gyrata* a German ostracod which had a ribbing pattern similar to that of *R. (R.) latior*. The only apparent difference is that Jones's figure indicates the presence of spines on the ribs. In a later paper, Jones (1890) described a new species, *Entomis richteri*, from a single specimen collected at Whiteway Farm (near localities WS1-5). This specimen, which is apparently now lost, measured 2×1.4 mm and had about fifteen ribs, only one of which

seems to be concentric in Jones's (1890, pl. xi, fig. 3) figure. The identity of *E. richteri* is unclear but it may have been based on an incomplete specimen of *R. (R.) latior*.

The Chinese specimens illustrated by Wang (1978) as *R. (R.) latior* have rather more numerous and less regularly arranged ribs than in typical European material. In these respects they are somewhat similar to *R. (R.) aff. latior* of Jordan and Bless (1970) and Gründel (1963).

Distribution. South-western England, Rheinische Schiefergebirge, Thüringia, European part of U.S.S.R. and possibly Kwangsi Province, China.

Richterina (Richterina) sp. 1

Text-figs. 4G, H

Material Studied. Two internal moulds: locality WS2 (AD2696, 2698B).

Dimensions.

Length (mm)	Height (mm)	L/H ratio
1.72	1.25	1.38
> 1.62	—	—

Description. The lateral outline is incompletely known but apparently broadly oval with equally rounded ends. The surface of the most complete specimen bears about thirty ribs across the greatest height. Approximately ten central ribs run parallel to the long axis and either end free or curve around at the ends of the valve. The remaining ribs run concentrically, parallel to the margin. There are some short, intercalated ribs. The rib spacing varies from 0.04 to 0.05 mm. One specimen has a small central muscle patch, interrupting a single rib. Internal moulds are ornamented by broad ribs separated by narrow grooves.

Discussion. The ribbing pattern of this form resembles that of *R. (R.) latior* but there are fewer inner longitudinal ribs and proportionally more outer concentric ribs. The various ostracods described under the name *R. (R.) aff. latior* either have fewer ribs (Sanchez de Posada and Bless, 1974) or more ribs (Gründel 1963; Jordan and Bless 1970) than *R. (R.) sp. 1*. Their ribbing is also less regular with fairly numerous intercalation and bifurcations. A specimen of *Maternella steinachensis* Gründel 1961 from the *Pericyclus* Stufe, illustrated by Gründel (1963, pl. 2, fig. 7), is rather similar to *R. (R.) sp. 1*.

Genus MATERNELLA Rabien, 1954

Type species. *Richterina(?) costata* var. nov. *dichotoma* Paeckelman, 1913.

Diagnosis. Lateral outline slightly asymmetrical and somewhat egg-shaped. Ventral margin more strongly curved than dorsal margin, posterior end more broadly rounded than anterior end. Maximum length just over half carapace height, maximum height and breadth somewhat behind mid-point. Sulcus not developed. More or less well-developed muscle patch lies at centre of sculpture. Strong, narrow ribs run concentrically or spirally, parallel to margin; in central part of valve ribs may run parallel to long axis. Weak cross-ribs or pits may be developed in intercostal grooves. Spines absent. (Modified after Rabien 1954, p. 134).

Discussion. The essential difference between *Maternella* and *Richterina* lies in the shape of the lateral outline which is symmetrical about the dorsal-ventral and anterior-posterior axes in *Richterina* but asymmetrical about these axes in *Maternella*.

A first step towards subdividing this unwieldy genus was taken by Gründel (1979) who established a new subgenus *Steinachella* for maternellids in which the ribs are not usually drawn out parallel to the long axis of the valve, but are arranged spirally or concentrically around the sculpture centre. An additional point is that all species of *M. (S.)* (with the possible exception, discussed below, of the problematical *M. psaffenbergensis*) have simple, low ribs, whereas in several species of *M. (M.)* the ribs are flange-like.

The nominate subgenus still includes a rather heterogenous array of species and it may ultimately be necessary to split the genus further.

Subgenus MATERNELLA (MATERNELLA) Rabien, 1954

Diagnosis. In central part of valve ribs are arranged more or less longitudinally or rhomboidally; variable number of ribs are concentric at ends of valve. Flange-like ribs may be developed. (Modified after Gründel 1979, p. 756.)

Discussion. As Gründel (1979, p. 757) pointed out, the ribbing patterns in the subgenera *Richterina* (*Richterina*) and *Maternella* (*Maternella*) show convergent trends which, in lower Carboniferous material, make them difficult to distinguish if the lateral outline is incomplete. It is also worth noting that in some lower Carboniferous species of *M. (M.)* the lateral outline, while showing more or less obvious anterior-posterior asymmetry (anterior end more narrowly rounded than posterior), appears, at least in British material, to have dorsal and ventral margins of approximately equal curvature, thereby deviating from the generic diagnosis. Lateral outlines of this kind have been observed in *M. (M.)* aff. *arcuata* (Pl. 74, figs. 3, 4), *M. (M.) clathrata* (Pl. 74, fig. 2; although Groos-Uffenorde 1974, p. 76 mentions an antero-ventral indentation of the margin), and *M. (M.) whitewayensis* sp. n. (see below). This point deserves further scrutiny.

Maternella (Maternella) aff. arcuata Gründel, 1961

Plate 74, figs. 3-4

v. 1974 *Maternella* cf. *arcuata* Gründel, 1961; Groos-Uffenorde, p. 74, pl. 2, fig. 5.

Material studied. Fourteen specimens: locality WS3 (AD2732, 2732A, 2765, 2766, 2768A, 2769, 2770).

Dimensions.

Length (mm)	Height (mm)	L/H ratio
2.10	1.55	1.35
1.60	1.15	1.43
1.45	1.10	1.32
1.10	0.80	1.38
1.10	0.80	1.38
1.00	0.75	1.33
0.85	0.65	1.31

Description of British material

Adults. The lateral outline is broadly oval, the dorsal and ventral margins are gently curved, and the ends broadly rounded and apparently symmetrical. The surface bears fifty to sixty fine concentric ribs separated by rather narrower grooves. In the outer part of the valve, the ribs are arranged parallel to the margin. Towards the interior they become more nearly longitudinal and follow an elongate, lenticular course which is sharply pointed at either end. A number of shorter ribs are intercalated between these inner and outer regions. The rib spacing varies from 0.022 to 0.032 mm. Fine cross-ribs with a spacing of 0.025-0.040 mm are clearly, although rather variably developed. At the centre of the ornamentation is a small, poorly defined muscle patch, about 0.10 mm diameter. Internal moulds have a well-developed ornamentation, similar to that on the outer surface.

Juveniles. Four specimens are probably juveniles. They are 0.85-1.10 mm long and have thirty-one to thirty-five ribs with a spacing of 0.022-0.025 mm.

Discussion. Unlike the species described by Gründel (1961, p. 133), this form has clearly developed cross-ribs and an apparently more symmetrical outline. The British material is identical to that described by Groos-Uffenorde (1974).

Some of the specimens illustrated by Jordan and Bless (1970, figs. 14-20) as *R. (R.)* aff. *laticor* are reminiscent of *M. (M.)* aff. *arcuata* but the ribbing is less regular and is not arranged in a clearly lenticular pattern in the central part of the valve.

Distribution. South-western England, Rheinische Schiefergebirge.

Maternella (Maternella) cf. circumcostata Rabien, 1960

Material studied. Three poorly preserved and incomplete internal moulds: localities WS2 (AD2696), TSI (AD3724, 3726; strongly deformed).

Dimensions. Approximate lengths: 1.60 mm (specimen lying parallel to tectonic stretching direction), 1.15 mm, 0.80 mm.

Description. The internal moulds have broad ribs separated by narrow grooves. There are twenty to thirty mostly spiral ribs across the height of the valve. In the central part of the valve, the ribs are lenticular, following a narrowly rounded or angular course at either end. The rib spacing is 0.05–0.06 mm.

Discussion. The three specimens are similar to *M. circumcostata*, as described by Rabien (1960, pp. 78–82) and Groos-Uffenorde (1974, p. 74), but are not well enough preserved to be positively identified.

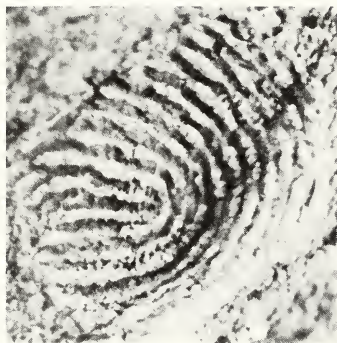
Maternella (Maternella) sp., aff. M. circumcostata Rabien, 1960 *sensu* Groos-Uffenorde (1974)

Text-fig. 5

v. 1974 *Maternella (Maternella) sp., aff. M. circumcostata* Rabien, 1960; *sensu* Groos-Uffenorde, pp. 74–75, pl. 5, figs. 4, 7; text-fig. 5.4–7.

Material studied. One incomplete external mould: locality TSI (AD3719).

Dimension. Approximately 1.40 mm.



TEXT-FIG. 5. External mould of *Maternella (Maternella) sp., aff. circumcostata* Rabien, 1960, *sensu* Groos-Uffenorde (1974), maximum dimension 1.40 mm, AD3719.

EXPLANATION OF PLATE 74

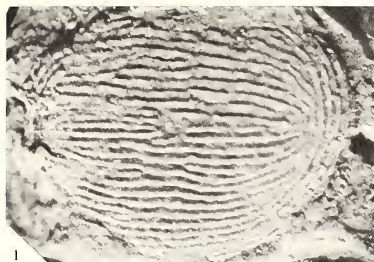
Fig. 1. *Richterina (Richterina) latior* Rabien, 1960. AD2697B, internal mould, maximum dimension 2 mm.

Fig. 2. *Maternella (Maternella) clathrata* (Kummerow, 1939), form 1. AD2770, internal mould, maximum dimension 2 mm.

Figs. 3, 4. *Maternella (Maternella) aff. arcuata* Gründel, 1961. 3, AD2770, internal mould, maximum dimension 2.10 mm. 4, AD2732, latex cast of external mould, maximum dimension 1.60 mm.

Fig. 5. *Maternella (Maternella) sp. 5 sensu* Groos-Uffenorde (1974). AD2692, external mould, width of upper part 1.75 mm.

Figs. 6, 7. *Maternella (Maternella) whitewayensis* sp. nov. 6, Holotype, AD2767, latex cast of external mould, maximum dimension 2.43 mm. 7, AD2729A, internal mould, maximum dimension 2.16 mm.



Description of British specimen. The external mould has broad ribs separated by intercostal grooves of similar width. There are eleven to twelve ribs between the centre and outer margin with a spacing of about 0.05 mm. They follow a spiral course which is approximately oval and more narrowly rounded at the anterior end. There are few intercalated ribs.

Discussion. The single specimen compares well with Groos-Uffenorde (1974) species. It is distinguished from *M. cf. circumcostata* by the broad ribs and the oval rather than lenticular course of the ribbing.

Distribution. South-western England, Rheinische Schiefergebirge.

Maternella (Maternella) clathrata (Kummerow, 1939)

Plate 74, fig. 2; text-fig. 6A-J

(?) 1879 *Entomis gyrata* (Rh. Richter, 1859); Jones, pl. xi, figs. 8a, b, 18a, b.

v* 1939 *Richterina (Richterina) clathrata* Kummerow, pp. 59-60, pl. 7, fig. 4.

(?) 1961 *Maternella gyrata* (Rh. Richter, 1859); Gründel, pp. 132-133, pl. 12, fig. 6.

v. 1974 *Maternella clathrata* (Kummerow, 1939); Groos-Uffenorde, p. 76, pl. 3, figs. 1, 2, 6; pl. 6; text-fig. 6.1-8.

Diagnosis. Relatively large species of *Maternella (Maternella)* with broadly oval lateral outline. Surface bears twenty to thirty-two (occasionally more) narrow ribs across height of valve, most of them following concentric, oval course, parallel to margin, with fairly numerous intercalated ribs towards centre. Variable number of ribs in outer part of valve often deflected outwards sigmoidally. Main ribs may be joined by weaker cross-ribs. Rib spacing: 0.035-0.083 mm. Central muscle patch interrupts several ribs.

Material studied. Form 1, about thirty-five specimens: localities WS2 (AD2695, 2695A, 2696, 2698A, 2698B), WS3 (AD2716, 2717, 2727, 2729B, 2729C, 2729D, 2730B, 2737-2739, 2753, 2754A, 2754B, 2759, 2766-2770, 2772, 2773). Form 2, three specimens: localities WS2 (AD2695, 2698A, 2698B), WS3 (AD2772B).

Dimensions.

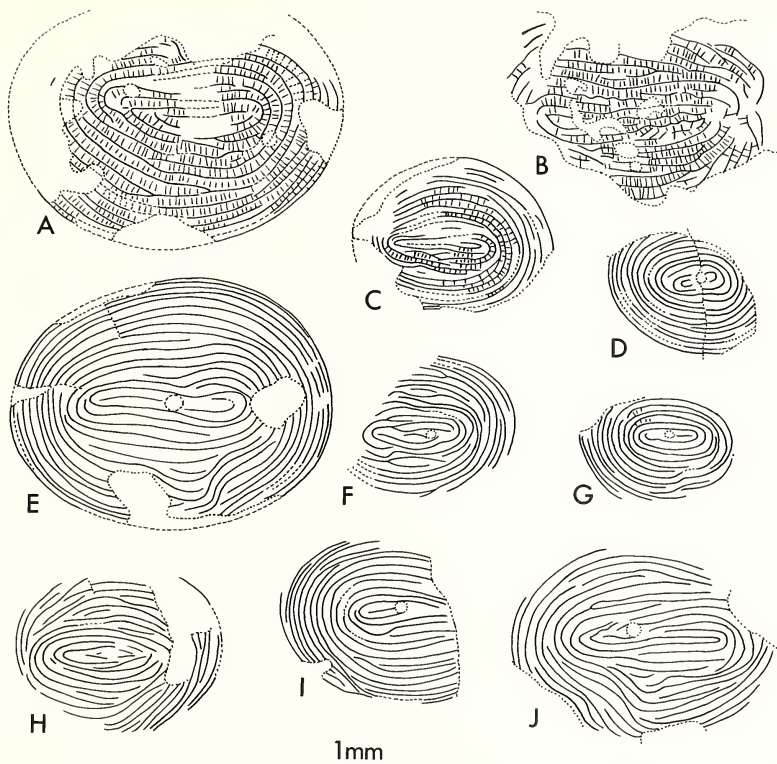
		Number of specimens	Range	Mean
Form 1	{ Length (mm)	10	0.80-2.00	1.30
	{ Height (mm)	10	0.75-1.20	1.05
	{ L/H ratio	10	1.23-1.40	1.36
Form 2	Length (mm)		Height (mm)	
	{ 2.15		> 1.17	
	{ 1.67		—	

Description of British material

There are two rather distinct forms.

Form 1. (Pl. 74, fig. 2; text-fig. 6D-J.) The lateral outline is broadly oval, the dorsal and ventral margins are gently curved, and the posterior end is more broadly rounded than the anterior end. The surface bears twenty to thirty-two narrow, mainly concentric ribs separated by broader intercostal grooves. In the outer part of the valve the ribs run parallel to the margin while towards the interior they are more nearly longitudinal, occasionally with a slight tendency to bend inwards on either side of the muscle patch. Near the end of the valve a variable number of ribs are often deflected outwards in an approximately sigmoidal pattern towards the margin but there is no evidence for a corresponding flexure of the margin. In the best-preserved specimen (text-fig. 6E) this deflection occurs near the posterior end. The rib spacing varies from 0.035 to 0.054 mm centrally, decreasing somewhat towards outside. Branched and intercalated ribs occur, particularly near the centre. Cross-ribs are not developed, or only weakly developed. A small central muscle patch is usually present. It is 0.075-0.150 mm in diameter and interrupts one to two ribs. Internal moulds bear broad ribs separated by intercostal grooves of similar width.

Form 2. (Text-figs. 6A-C.) This form is characterized by the presence of well-developed cross-ribs and a tendency for several pairs of inner ribs to meet anteriorly at an acute angle. The rib spacing of the best-preserved specimen is broader (0.05-0.083 mm) than in form 1.



TEXT-FIG. 6. *Maternella (Maternella) clathrata* (Kummerow, 1939). A-C, form 2: A, AD2695, internal mould; B, AD2698A, external mould; C, AD2772B, internal mould. D-J, form 1, all external moulds except where stated otherwise: D, AD2769; E, AD2770, internal mould; F, AD2696; G, AD2754A; H, AD2698B; I, AD2729C; J, AD2696.

Discussion. Kummerow's (1939) holotype of *M. (M.) clathrata* has been examined and is closely similar to form 2 while many of the specimens assigned by Groos-Uffenorde (1974) to this species are certainly conspecific with form 1. In the British material these two varieties seem distinct but Groos-Uffenorde's (1974, text-fig. 6) specimens clearly demonstrate their intergradation.

R. (M.) gyrata of Gründel (1961), and some of the specimens described by Jones (1879) as *Entomis gyrata* are close to *M. (M.) clathrata* in lateral outline and ribbing pattern although the synonymies cannot be confirmed. *R. (R.) kiliginae* Posner, 1958, *M. n. sp.* 3 of Groos-Uffenorde (1974), and *M. (M.) n. sp.* of Gründel (1979) all have more ribs than *M. (M.) clathrata*.

Distribution. South-western England, Rheinische Schiefergebirge and possibly Thüringia.

Maternella (Maternella) sp. 5 sensu Groos-Uffendorde (1974)

Plate 74, fig. 5; text-fig. 8D

vp. 1974 *Maternella sp. 5* Groos-Uffendorde, p. 80, pl. 3, fig. 3 (not pl. 6 = *M. (M.) whitewayensis sp. nov.*).*Material studied.* Two specimens: locality WS2 (AD2695, 2692).*Dimensions.*

	Length (mm)	Height (mm)
AD2695	> 2.35	> 2.25
AD2692	> 1.75	> 2.14

Description of British material. The carapace outline is not known. The surface bears fairly narrow ribs separated by broad, flat intercostal spaces. The ribs follow an approximately lenticular course and, in the central part of the valve, several meet anteriorly and posteriorly at an acute angle. In the outer part of the valve, the ribs are more evenly curved and probably run parallel to the margin. Intercalated ribs are fairly numerous. The rib spacing ranges from 0.06 mm to 0.13 mm. At the centre of the ornamentation is a circular muscle patch, about 0.075 mm in diameter, which interrupts at least one rib. Internal moulds have broad ribs separated by narrow grooves.

Discussion. Apart from the more clearly lenticular arrangement of the ribs around the central muscle patch, the two British specimens are similar to the external mould illustrated by Groos-Uffendorde (1974, pl. 3, fig. 3).

Distribution. South-western England, Rheinische Schiefergebirge.

Maternella (Maternella) whitewayensis sp. nov.

Plate 74, figs. 6-7; text-figs. 7A-D

v. 1961 *Richterina (Richterina)? cf. enpleura* Kummerow, 1939; Gründel, pp. 126-127, pl. 11, fig. 7.vp. 1974 *Maternella sp. 5* Groos-Uffendorde, p. 80, pl. 6 (not pl. 3, fig. 3).

Derivation of name. From Whiteway Barton, Kingsteignton, Devon.

Holotype. Internal mould (AD2766) and corresponding external mould (AD2767), both incomplete; text-fig. 7A and Pl. 74, fig. 6.

Type locality. WS3: SX88577553; trench trending 146° parallel to north-eastern edge of field between SX88577533 and SX88567555, beginning 24.6 m from north-western edge of field running south-eastward for 30.4 m at distance of 3.6 m from north-eastern edge of field. Material collected from south-eastern end of trench to 5.2 m along it in a north-westerly direction.

Horizon. Middle *Gattendorfa*-Stufe.

Other material studied. Only from the type locality; four corresponding internal and external moulds (AD2701, 2702, 2729A, 2729D, 2769, 2770, 2772, 2773), two external moulds (AD2700, 2761), two internal moulds (AD2754A, 2760).

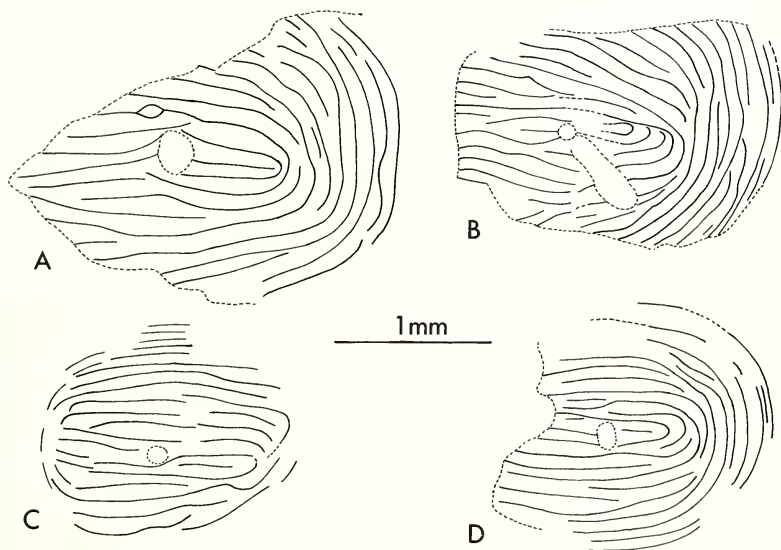
Diagnosis. Large species of *Maternella (Maternella)* (length > 2 mm) with fairly elongate lateral outline. Surface bears approximately twenty to thirty-five ribs across height. Inner ribs more or less longitudinal, outer six to seven ribs run concentrically. Rib spacing fairly wide: 0.05-0.10 mm. Central muscle patch relatively large, and slightly depressed. Shallow, sulcus-like structure (?original) may be developed.

Dimensions.

Specimen	Reg. no.	Length (mm)	Height (mm)	L/H ratio
Fairly complete ext. mould	AD2700	2.12	1.51	1.40
Fragmentary ext. mould	AD2701	1.71	1.08	
Fragmentary int. mould	AD2702	1.71	1.08	
Fairly complete int. mould	AD2729A	2.16	1.71	1.26

Specimen	Reg. no.	Length (mm)	Height (mm)	L/H ratio
Fragmentary ext. mould	AD2729D	1.79	1.35	
Fragmentary int. mould	AD2754A	1.53	1.35	
Fairly complete int. mould	AD2760	1.97	1.58	1.25
Fairly complete ext. mould	AD2761	2.07	1.44	1.44
{ Holotype int. mould	AD2766	2.56	2.07	
{ Holotype ext. mould	AD2767	2.43	1.84	
{ Fragmentary int. mould	AD2769	2.16	1.71	
{ Fragmentary ext. mould	AD2770	2.03	1.53	
{ Complete int. mould	AD2772	2.07	1.53	1.35
{ Incomplete ext. mould	AD2773	1.80	1.49	

Description. The lateral outline is broadly oval with a mean L/H ratio of 1.37. None of the specimens is complete, but those which are most complete appear to be rather more narrowly rounded at the anterior end. The dorsal and ventral margins seem to be of approximately equal curvature. The surface bears twenty-three to thirty-two narrow ribs which follow a rather irregular course and are separated by broad, shallow intercostal grooves. Six or seven outer ribs run concentrically. Shorter ribs are intercalated, particularly near the centre of the valve. In some specimens, for example the holotype, it can be clearly seen that the ribs extend a short distance from the valve surface as flange-like structures. The rib spacing is wide; in five specimens it averages 0.055 mm, 0.066 mm, 0.070 mm, 0.093 mm, and 0.100 mm. There is a smooth, slightly depressed central muscle patch, 0.15–0.25 mm in diameter, which interrupts two or three ribs. Several specimens have a shallow, sulcus-like structure extending down from the ?dorsal margin towards the centre of the valve. This may not be an original feature. The ornamentation of internal moulds is similar to that of the outer surface except that the ribs are rather broader.



TEXT-FIG. 7. *Maternella (Maternella) whitewayensis* sp. nov., external moulds. A, Holotype, AD2767. B, AD2770. C, AD2729D. D, AD2773.

Discussion. This species resembles *M. grammica* (Kummerow, 1939) in size, ribbing pattern, the presence of a somewhat depressed muscle patch, and, in some specimens, of a shallow, sulcus-like structure (see Rabien 1960, p. 84). Kummerow's (1939) specimens of *M. grammica*, and its synonym *M. lenticularis* (Kummerow, 1939), have been examined. They differ from *M. whitewayensis* in having a more rounded lateral outline ($L/H = 1.1-1.3$ according to Rabien 1960), somewhat fewer ribs with a correspondingly wider rib spacing, and a triangular or lenticular, rather than longitudinal, arrangement in the central part of the valve. The ribs in *M. grammica* also appear to be more prominently flange-like than those of *M. whitewayensis*. Another similar form, *M. empleura* (Kummerow, 1939) (holotype examined), is smaller (length = 1.44 mm) than the new species and has more regular ribbing.

There are specimens of *M. whitewayensis* in Groos-Uffenorde's (1974) material of '*M. sp. 5*' from the upper *Gattendorfia* Stufe (Stockum samples 924, 930). However, specimens from the base of the middle *Gattendorfia* Stufe (sample 916) belong to a distinct species, described above.

Distribution. South-western England, Rheinische Schiefergebirge, Thüringia.

Subgenus MATERNELLA (STEINACHELLA) Gründel, 1979

Type species. *Richterina (Maternella) steinachensis* Gründel, 1961.

Diagnosis. Ribs arranged spirally or concentrically around sculpture centre and not drawn out parallel to long axis of valve. Ribs never flange-like. (Modified after Gründel 1979, p. 757.)

Discussion. This subgenus includes the following species: *Maternella geniceraensis* Jordan and Bless, 1970; ?*Graphiodactylus gyripunctuatus* Kummerow, 1939; *Richterina (Maternella) rabieni* Gründel, 1961; *Maternella rotundata* Tschigova, 1977; *Graphiodactylus schindewolfi* Kummerow, 1939 (= *Richterina (Maternella) circumcostatula* Koch, 1970); *Richterina (Maternella) seilerensis* Koch, 1970; *Richterina (Maternella) steinachensis* Gründel, 1961; *Maternella sp. 4 sensu* Groos-Uffenorde, 1974.

The list is the same as that given by Gründel (1979, p. 757) except for (i) the inclusion of *M. rotundata*, (ii) the exclusion of *R. (M.) pfaffenbergensis*, and (iii) the confirmation of the synonymy between *R. (M.) circumcostatula* and *G. schindewolfi*. As discussed by Gründel (1979, p. 758), *R. (R.) ampla* Gründel, 1963 may belong in this subgenus.

Maternella (Steinachella) schindewolfi (Kummerow, 1939)

v* 1939 *Graphiodactylus schindewolfi* Kummerow, pp. 33-34, pl. 3, fig. 10.

1970 *Richterina (Maternella) circumcostatula* Koch, pp. 722-724, pl. 9, figs. 3-4.

v. 1974 *Maternella schindewolfi* (Kummerow, 1939); Groos-Uffenorde, pp. 78-79, pl. 2, figs. 1-3.

Material studied. Twenty-nine specimens: locality WS3 (AD2700, 2710, 2711, 2729E, 2729F, 2730, 2730A, 2730B, 2730C, 2737, 2740, 2753, 2754A, 2766, 2767, 2768, 2768A, 2768B, 2769).

Dimensions.

	Number of specimens	Range	Mean
Length (mm)	12	0.95-1.75	1.30
Height (mm)	12	0.70-1.20	0.98
L/H ratio	12	1.18-1.48	1.32

Diagnosis. Species of *Maternella (Steinachella)* with numerous concentric ribs, very fine and closely spaced in inner part of valve, becoming more widely spaced towards margin. In centre of valve fine ribbing is arranged about axis at angle of 45-90° to long axis; outside immediate centre, ribbing is parallel to margin. There is no muscle patch.

Description of British material. The lateral outline is broadly and asymmetrically oval. The dorsal margin is gently curved and the ventral margin rather strongly curved. The posterior end is broadly and symmetrically rounded and the anterior end is more narrowly rounded with the extremity above the mid-point. The surface

bears about sixty concentric ribs across the height of the valve. In the outer part they are relatively strong with a spacing of 0.025–0.035 mm, and conform to the margin. Towards the centre, the ribs become very fine and closely spaced (0.012–0.015 mm) and usually follow an approximately subtriangular course, except in the immediate centre where they are arranged in an oval, the long axis of which lies at 45–90° to the length of the valve. However, in one specimen the inner ribbing is oval rather than subtriangular and the long axis is arranged horizontally. The tendency for coarser outer ribbing to pass into finer ribbing is not uniform in all directions. In some parts of the valve, usually near one end, fine ribs may persist to near the margin, while elsewhere the coarser ribbing extends inwards to half-way between the margin and the mid-point. Thus, over the outer quarter to one-half of the valve surface, areas of fine ribbing give way to areas of coarser ribbing. At the junction between these two types of ornament, the coarse ribs rapidly become narrow and pass into fine ribs between which are intercalated additional fine ribs. A muscle attachment area has not been observed. Internal moulds have fairly strong ribbing similar to that on the outer surface.

Discussion. Groos-Uffenorde (1974, p. 78) regarded *Richterina* (*Maternella*) *circumcostatula* as a junior synonym of *Graphiodactylus schindewolfi* but the synonymy was questioned by Gründel (1979, p. 758). According to Kummerow's (1939, pl. 3, fig. 10) illustration, *G. schindewolfi* has a more elongate lateral outline and inner, fine ribbing which is arranged about an approximately horizontal axis, rather than obliquely or dorso-ventrally as in *R. (M.) circumcostatula*. The ornamentation of the British specimens conforms well with the *R. (M.) circumcostatula* pattern except in one case (described above) where it is more similar to that of *G. schindewolfi*. Groos-Uffenorde (1974, pl. 2, fig. 1) illustrated an external mould having a moderately elongate carapace and ornamentation resembling the *G. schindewolfi* pattern fairly closely. My notes on the holotype of *G. schindewolfi* (an internal mould), examined in 1974 before the publication of Groos-Uffenorde's and Gründel's papers, record that the ribbing, although difficult to see, is close to that of *R. (M.) circumcostatula*. For these reasons it seems likely that the holotype of *G. schindewolfi* falls within the morphological range of *R. (M.) circumcostatula* and the synonymy of these two species is therefore accepted.

In the specimens described by Koch (1970) and Groos-Uffenorde (1974) the outer ribs are more widely spaced and more sharply differentiated from the fine inner ribbing than in the British material. It is considered that these differences arise from intraspecific variability and are of no taxonomic significance.

Although not clearly shown in Gründel's (1961, pl. 12, fig. 1a, b) figures, the holotype of *M. (S.) steinachensis* Gründel, 1961 has ribs which, in the centre, are arranged about an axis lying at approximately 40° to the length of the valve. This is very similar to the arrangement in *M. (S.) schindewolfi*. The only significant difference between the two species is the uniform strength of the ribbing in *M. (S.) steinachensis*.

Distribution. South-western England, Rheinische Schiefergebirge.

Maternella (*Steinachella*) *seilerensis* Koch, 1970

Text-fig. 9A–D

* 1970 *Maternella seilerensis* Koch, pp. 725–726, pl. 10, fig. 2.

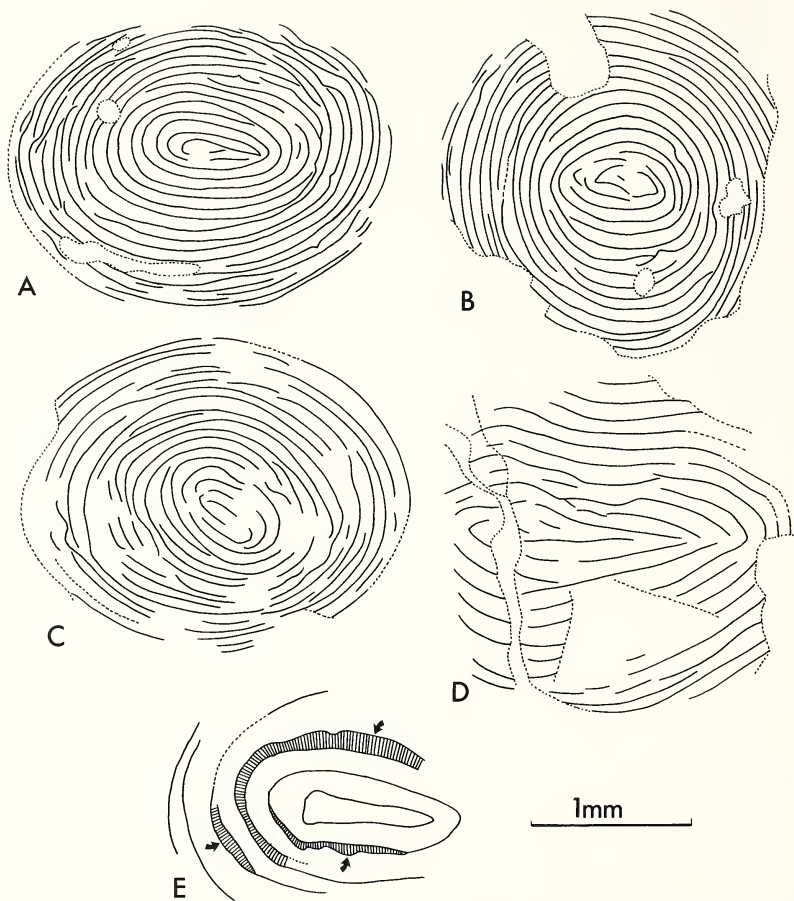
v. 1974 *Maternella* sp. 4 *sensu* Groos-Uffenorde, p. 80, pl. 2, fig. 7; pl. 4, fig. 6.

Material studied. Twenty-three specimens: locality WS3 (AD2732, 2738, 2751, 2758, 2759, 2761, 2764, 2765, 2767–2770, 2770A).

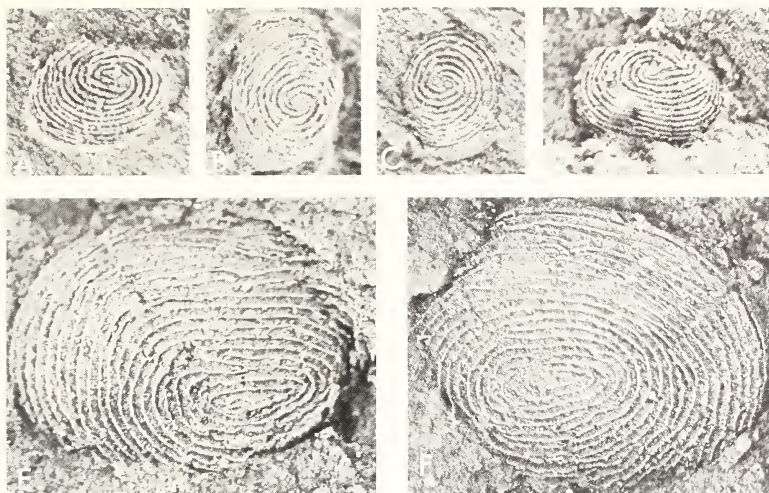
Dimensions.

	Number of specimens	Range	Mean
Length (mm)	7	0.45–0.80	0.65
Height (mm)	7	0.40–0.65	0.51
L/H ratio	7	1.20–1.37	1.27

Diagnosis. Rather small species of *Maternella* (*Steinachella*) with circular to broadly oval outline. Surface bears two to three spiral ribs running approximately parallel to margin; twenty-two to



TEXT-FIG. 8. A-C, *Maternella* (*Steinachella*) sp. 1. A, ZO4390, external mould. B, ZO4394, external mould. C, ZO4391, internal mould. D, *Maternella* (*Maternella*) sp. 5 *sensu* Groos-Uffenorde (1974), AD2695, internal mould. E, *Maternella* (?Subgenus) *pfaffenbergensis* Gründel, 1961. AD2717, internal mould, arrows indicate distal (outer) edges of flange-like ribs.



TEXT-FIG. 9. A-D *Maternella (Steinachella) seilerensis* Koch, 1970. A, AD2770A, external mould, maximum dimension 0.70 mm. B, AD2769, internal mould, maximum dimension 0.90 mm. C, AD2770, latex cast of external mould, maximum dimension 0.50 mm. D, AD2769, latex cast of external mould, maximum dimension 0.75 mm. E, F, *Maternella (Steinachella)* sp. 1. E, ZO4390, maximum dimension 2.15 mm. F, ZO4391, maximum dimension 2.25 mm.

thirty-six ribs can be counted across height of valve. Rib spacing decreases towards margin. Small, central muscle patch developed.

Description of British Material

Adults. The lateral outline is broadly oval. The surface bears two to three broad, spirally arranged ribs, separated by narrow intercostal grooves. The ribs make three to four revolutions and twenty-six to thirty-six can be counted across the height of the valve. They follow an almost circular to moderately oval course with a spacing of 0.028–0.035 mm near the centre, decreasing to 0.022–0.025 mm towards the margin. A number of ribs bifurcate. At the centre of the valve is a small muscle patch, 0.04–0.06 mm in diameter. The ornamentation of internal moulds is similar to that of the external surface.

Juveniles. A small, nearly circular specimen, 0.45 mm in diameter, with about twenty-five ribs, is probably a juvenile.

Discussion. In his description of *M. seilerensis* Koch (1970, p. 725) states that the ornamentation comprises an inner spiral rib which is finer than the outer concentric ribbing. It was because of this that Groos-Uffenorde (1974, p. 80) separated *M. seilerensis* from *Maternella* sp. 4 in which the outer ribbing is finer than the inner. However, Koch's (1970, pl. 10, fig. 2) photograph of the holotype does not correspond to his description because the outer ribs are clearly more closely spaced than the inner ribs. The holotype differs from Groos-Uffenorde's form, and from most of the British material, in having a more circular outline, but this may be an ontogenetic effect since the smallest British specimen (slightly smaller than the holotype) is also nearly circular.

Distribution. South-western England, Rheinische Schiefergebirge.

Maternella (Steinachella) sp. 1

Text-figs. 8A-C, 9E, F

Material studied. Five specimens: locality BLF1 (ZO4390, 4391, 4394).*Dimensions.*

Length (mm)	Height (mm)	L/H ratio
2.37	1.92	1.23
2.37	1.92	1.23
2.32	2.02	1.14
> 2.25	> 1.75	—

Description. The lateral outline is broadly oval. Details are unknown but the ribbing pattern suggests that the anterior end is more narrowly rounded than the posterior end. The surface bears narrow ribs, separated by broader intercostal grooves and following a spiral course which is more narrowly rounded at the anterior end and apparently conforms to the margin. There are thirty-four to forty-two ribs across the height of the valve with a spacing between 0.042 and 0.060 mm. A number of ribs are intercalated or bifurcate. Internal moulds bear a vague ornamentation of indistinct ribs.

Variation. In three specimens, the central ribbing follows an elongate oval course (text-fig. 8A) but in two specimens it is less elongate (text-fig. 8B). One internal mould is unusual because the ribs in the inner part of the valve are arranged about an axis lying at approximately 45° to the horizontal (text-fig. 8C).

Discussion. This distinctive ostracod has a ribbing pattern similar to that of *M. (M.) sp. aff. circumcostata sensu* Groos-Uffenorde (1974) but is rather larger and, more importantly, the ribs are considerably narrower, rather than broader than the intercostal grooves. *M. (S.) sp. 1* is distinguished from *M. (S.) geniceraensis* Jordan and Bless, 1970 by the greater regularity of the ribbing, by the smaller number of ribs, and, in at least some specimens, by the somewhat more elongate course of the central ribbing.

Distribution. South-western England.

Maternella (?Subgenus) *pfaffenbergensis* Gründel, 1961

Text-fig. 8E

- v* 1961 *Richterina (Maternella) pfaffenbergensis* Gründel, pp. 131–132, pl. 12, fig. 5.
v. 1974 *Maternella pfaffenbergensis* Gründel, 1961; Groos-Uffenorde, p. 78, pl. 2, fig. 4.

Diagnosis. Large species (length up to 2 mm), with broadly oval lateral outline, anterior end more narrowly rounded than posterior. Surface bears few flange-like ribs which follow elongate spiral or concentric course, more narrowly rounded at anterior end. There are five to six ribs between central muscle patch and margin. Rib spacing is very wide: 0.15–0.20 mm. (Modified after Gründel 1961.)

Material studied. Seven incomplete specimens: locality WS3 (AD2714, 2716, 2717, 2756, 2757).

Dimensions.

Length (mm)	Height (mm)	L/H ratio
1.80	1.50	1.20
1.85	1.55	1.19
1.90	1.70	1.12

Description of British material. The lateral outline is not preserved. The surface bears one or more spiral or concentric flange-like ribs extending to a height of >0.10 mm. Between the centre and margin of the valve there are at least four ribs separated by broad, flat intercostal spaces, and following a course which is more strongly curved on the ventral side and more narrowly rounded at the anterior end. Near the valve centre there may be one or two intercalated ribs. The rib spacing varies from 0.11 to 0.20 mm. The ribs deviate around a large circular central muscle patch, about 0.20 mm in diameter. Internal moulds are ornamented by a shallow spiral groove corresponding to the rib on the outer surface.

Discussion. The subgeneric placement of this species is problematical. It conforms to the diagnosis of *M. (Steinachella)* in having spirally or concentrically arranged ribs. On the other hand, *M. pfaffenbergensis* has at least two characters in common with species of *M. (Maternella)*: the flange-like structure of the ribs and their drawing out parallel to the long axis of the valve. Gründel (1979, p. 758) regarded it as being a morphological link between *M. (M.) hemisphaerica* (Rh. Richter, 1848) and *M. (S.) rabieni*. *R. (M.) gruendeli* Koch, 1970, is a closely similar species in which the ornamentation is intermediate between that of *M. (M.) hemisphaerica* and *M. (?Subgenus) pfaffenbergensis*.

Distribution. South-western England, Rheinische Schiefergebirge, Thüringia.

KUZMINAELLA Tschigova, 1977

Type species. *Kuzminaella venusta* Tschigova, 1977.

Diagnosis. Similar to *Maternella* but with ribs following irregular, swirling course. Cross-ribs may be developed.

?*Kuzminaella* sp.

Text-fig. 10

Material studied. Single, fragmentary external mould (AD2728) and part of corresponding internal mould (AD2727); locality WS3.

Dimension. The maximum dimension of the fragment is 3.45 mm.

Description. The fragment is basically semicircular in outline, the curved border being the original margin of the valve. It is slightly buckled tectonically and the external mould is disrupted by a tear-like dislocation. The surface bears ribs (spacing 0.045–0.095 mm) following an irregular, curved course with no clear pattern. They run parallel to the margin for a short distance, but in general impinge upon the margin at a shallow angle. There are numerous intercalated ribs. Examined in detail, the 'ribs' are seen to comprise several elements. Narrow, irregular, flange-like ribs extend out from the valve surface and to one side of these are much broader, low, ridge-like structures (broad, shallow grooves on the external mould) which are separated from the next flange-like rib by a somewhat broader intercostal groove. The broad ridges become less prominent towards the margin.

Remarks. The disorganized, rather swirling ribbing pattern of this fragment is similar to that of *Kuzminaella* (see particularly Tschigova 1977, pl. xiii, fig. 6), although the specimen is considerably larger than any of Tschigova's (1977) species.

Subfamily ENTOMOPRIMITIINAE Gründel, 1962

Diagnosis. Lateral outline usually asymmetrical and broadly oval with clearly developed straight dorsal margin. Ribs arranged concentrically, usually following elliptical or triangular pattern around sculpture centre. (After Gründel 1962, p. 1203.)

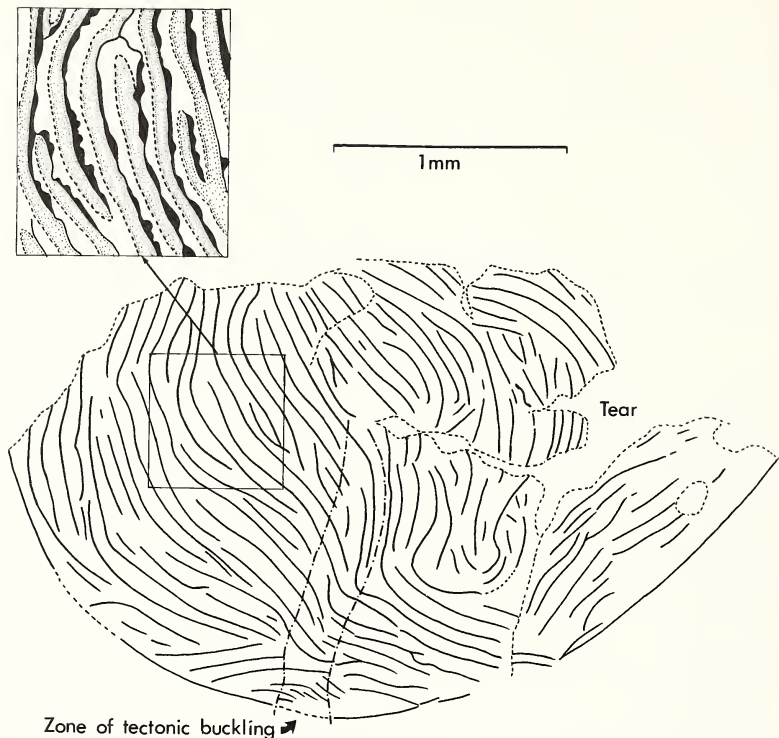
Discussion. The Entomoprimitiinae includes two genera and their subgenera: *Entomoprimitia* (*Entomoprimitia*) Kummerow, 1939; *E. (Reptiprimitia)* Gründel, 1962; *Bertillonella* (*Bertillonella*) Stewart and Hendrix, 1945; *B. (Rabienella)* Gründel, 1962.

Genus BERTILLONELLA Stewart and Hendrix, 1945

1954 *Waldeckella* Rabien.

Type species. *Bertillonella subcircularis* Stewart and Hendrix, 1945.

Diagnosis. Lateral outline asymmetrical and broadly oval to droplet-shaped with short, straight dorsal margin and anterior end more gently rounded than posterior end. Sulcus-like depression in anterior one-third of dorsal margin. Concentric ribs arranged in elliptical, subtriangular, or



TEXT-FIG. 10. ?*Kuzminaella* sp., AD2728, external mould. The inset shows the ornamentation in more detail: the black areas are the exposed faces of flange-like ribs; the stippled areas are shallow depressions; the white areas are low ridges.

subrectangular course around muscle patch: one species with rows of minute spines centred around antero-dorsal sculpture centre. (Based on Rabien 1954, p. 150.)

Discussion. The broader end of the carapace in *Bertillonella* has been interpreted as the anterior. This orientation, which is based on the position nearer the broader end of the dorsal depression (?rudimentary sulcus), should be regarded as questionable because in all other entomozoaceans with asymmetrical outlines, including *Entomoprimitia*, the anterior end is narrower than the posterior end.

Subgenus BERTILLONELLA (BERTILLONELLA) Stewart and Hendrix, 1945

Diagnosis. Lateral outline asymmetrical and broadly oval. Concentric ribs arranged in elliptical course around muscle patch with long axis of ellipse parallel, or at right angles to long axis of carapace. (Based on Gründel 1962, p. 1200.)

Bertillonella (*Bertillonella*) sp. 2 *sensu* Groos-Uffenorde, 1974

v. 1974 *Bertillonella* (*Waldeckella*) sp. 2 *sensu* Groos-Uffenorde, p. 73, text-fig. 4.

Material studied. Nine strongly deformed internal and external moulds: locality TS1 (AD3721, 3722, 3727, 3729, 3730).

Dimensions.

	Number of specimens	Range	Mean
Length (mm)	6	0.45-0.70	0.59
Height (mm)	6	0.50-0.85	0.62
L/H ratio	6	0.59-1.30	0.90

Description of British material. The outline is unknown. The height of the valve is approximately equal to the length or occasionally exceeds the length, probably as the result of tectonic distortion. The surface bears several spirally arranged ribs which follow an oval course, at right angles to the length of the valve. Between twenty-four and thirty-two ribs can be counted across the height. The rib spacing ranges from 0.022 to 0.030 mm. Weak cross-ribs may be developed. A muscle patch has not been observed. Internal moulds are indistinctly ornamented.

Discussion. The strongly deformed British material compares well with that of Groos-Uffenorde (1974). This small form is distinguished from species of *Maternella* by the arrangement of the ribbing about a dorsal-ventral axis.

Distribution. South-western England, Rheinische Schiefergebirge.

Family RHOMBOENTOMOZOIDAE Gründel, 1962

Type genus. *Rhomboentomozoe* Přibyl, 1949.

Diagnosis. Valves of apparently equal size. Lateral outline triangular to subquadrate, sometimes broadly egg-shaped. Straight dorsal margin usually well developed, sometimes corresponding to greatest carapace length; dorsal angles distinct or rounded. Sulcus always present, usually strongly developed, often extending across more than half of valve surface. Muscle attachment area absent. Spines may be developed near margin. Ornamentation comprises longitudinal ribs arranged parallel to dorsal margin, some outer ribs may be parallel to ends of valve. Surface occasionally smooth. (Slightly modified after Gründel 1962, p. 1198.)

Discussion. In addition to the type genus, the family includes *Pseudoentomozoe* Přibyl, 1949, *Ungerella* Livental, 1948, and possibly *Vltavina* Bouček, 1936. It is distinguished from the Entomozooidae by the generally triangular to subquadrate lateral outline and the long, straight dorsal margin.

Genus UNGERELLA Livental, 1948

1954 *Franklinella* Rabien, 1954.

Type species. *Cypridina calcarata* Rh. Richter, 1856.

Diagnosis. Carapace thin and weakly calcified. Lateral outline broadly egg-shaped, subquadrate, or triangular with greatest height in middle to anterior third and greatest length above mid-height. Straight dorsal margin usually clearly developed. Dorsal angles rounded. Anterior end more broadly rounded than posterior end. Sulcus prominent and deep, beginning in middle dorsal margin and curving across more than three-quarters of valve surface. Valve bears two obliquely directed spines, larger one situated at antero-ventral corner, smaller one postero-dorsal; antero-ventral spine is often in line with end of sulcus. Surface bears longitudinal ribs, some of which converge towards spines, others continue parallel to ends of valve. Number, spacing, and precise arrangement of ribs varies widely. (Modified after Rabien's 1954, p. 46 diagnosis of *Franklinella*.)

Discussion. *Ungerella* differs from *Rhombentomozoe* in the presence of two (antero-ventral and postero-dorsal) spines rather than one (ventral) spine. *Pseudoentomozoe* lacks spines and, like *Rhombentomozoe*, it has a more triangular outline than *Ungerella*.

Ungerella aff. *postmulticostata* Groos-Uffenorde, 1974

Text-figs. 11A, B

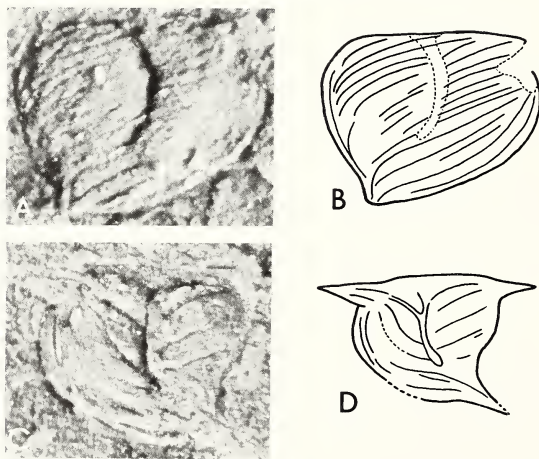
Material studied. Nine specimens: locality WS3 (AD2731, 2768, 2769, 2770).

Dimensions.

	Number of specimens	Range	Mean
Length (mm)	6	0.35-0.55	0.48
Height (mm)	6	0.25-0.45	0.37
L/H ratio	6	1.22-1.50	1.31

Description. The lateral outline is rounded and approximately subquadrate. The dorsal margin is fairly straight and occupies more than three-quarters of the valve length. The posterior end is rather more narrowly rounded than the anterior end and joins the gently curved ventral margin evenly. Just below the postero-dorsal margin is a short, conical spine which is directed slightly outwards and upwards. A similar spine arises from just inside the antero-ventral margin. The narrow, fairly deep sulcus extends across two-thirds to three-quarters of the valve surface and its lower part is directly in line with the antero-ventral spine.

The surface bears sixteen to eighteen narrow ribs separated by wider, flat intercostal spaces. The ribs run longitudinally, parallel, or at a slight angle to the dorsal margin and tend to converge towards the spines. One or two ribs are concentric around the posterior end and one rib runs parallel to the anterior end. There is no deviation of the ribs across the sulcus. The rib spacing ranges from 0.022 to 0.025 mm. Internal moulds are ornamented by shallow grooves which correspond to the ribs on the external surface.



TEXT-FIG. 11. A, B, *Ungerella* aff. *postmulticostata* Groos-Uffenorde, 1974, AD2769. A, photograph of internal mould, maximum dimension 0.50 mm and B, interpretation. C, D, *Ungerella stockumensis* Groos-Uffenorde, 1974, AD2768. C, Photograph of internal mould and D, interpretation.

Discussion. The British specimens are close to *U. postmulticostata* but are usually smaller, with a less elongate lateral outline, fewer longitudinal ribs, and a rather more prominent postero-dorsal spine.

Ungerella stockumensis Groos-Uffenorde, 1974

Text-fig. 11c, d

v* *Ungerella stockumensis* Groos-Uffenorde, p. 84, pl. 5, figs. 1-2, text-fig. 7.6-11.

Material studied. Six specimens: locality WS3 (AD2768, 2768A, 2769, 2770).

Dimensions.

Length (mm)	Height (mm)	L/H ratio
0.60	0.43	1.39
0.55	—	—
0.57	0.43	1.33
> 0.40	0.37	—
0.60	0.37	1.62

Diagnosis. Medium-sized *Ungerella* with very well-developed ventral spine, few narrow ribs, and broad intercostal spaces. On both sides, ribs make more or less acute angle with sulcus. (After Groos-Uffenorde, 1974.)

Description of British material. The lateral outline is approximately subquadrate with a long and fairly straight dorsal margin. The best-preserved internal and corresponding external moulds bear two large spines at the ends of the dorsal margin. The prominent antero-ventral spine projects out at an angle of about 45° to the dorsal margin for at least 0.15 mm. The sulcus is well developed, narrow, and deep, extending across two-thirds to three-quarters of the valve surface and, at its ventral end, directly in line with the antero-ventral spine.

The surface bears six or seven narrow, flange-like ribs separated by broad intercostal spaces. Behind the sulcus four ribs follow a curved course, parallel to the posterior and ventral margins; at least one of these ribs continues on to the antero-ventral spine. One or two of the more dorsal ribs on the posterior side of the sulcus run at an angle of 45° or less to the dorsal margin. In front of the sulcus the ribs are approximately straight and follow a more nearly longitudinal course at an angle of 20 to 30° to the dorsal margin, ending against the anterior margin and the sulcus. The rib spacing varies from 0.075 to 0.10 mm. Between the main ribs, there may be a number of very narrow, closely spaced riblets. Internal moulds are ornamented by shallow grooves which correspond to the ribs on the external surface.

Discussion. The presence of what appear to be spines at both the anterior and posterior ends of the dorsal margin is of particular interest because ungerellids with three spines have been reliably documented only once (Rabien 1954, p. 61, in several specimens of *Franklinella*? (= *Ungerella*) aff. *calcarata*; see also p. 48). However, the additional antero-dorsal spine is visible in only one of the specimens and its exact nature is uncertain. Apart from the possible development of two dorsal spines, the British specimens agree well with Groos-Uffenorde's (1974) description of *Ungerella stockumensis*.

Distribution. South-western England, Rheinische Schiefergebirge.

THE STRATIGRAPHIC DISTRIBUTION OF CARBONIFEROUS ENTOMOZOACEA

European distribution. In Europe, Carboniferous entomozoaceans have usually been collected from relatively restricted sections although in many cases the ostracod-bearing horizons can be dated by means of conodonts or ammonoids. By combining sections, it is therefore possible to establish the general stratigraphic distribution of species within the system (Groos-Uffenorde, in press) and demonstrate that the Entomozoacea range just into the upper Carboniferous but are most abundant and diverse in the Tournaisian.

The number (ignoring accepted synonymies and cf. determinations) of named species and open nomenclature forms of different genera described from the topmost upper Devonian and different stratigraphic divisions of the Carboniferous in Europe are set out in Table 1. According to this compilation, there is apparently little fundamental change in the entomozocean fauna across the Devonian–Carboniferous boundary apart from the appearance of numerous new species of *Maternella* in the lower Tournaisian and the reappearance of the Frasnian and lower Famennian genera *Bertillonella* and *Ungerella*. This agrees with the conclusion of Groos-Uffenorde (in press) that 'in spite of the occurrence of new species there is no prominent biotic change at the Devonian–Carboniferous boundary within the entomozoids . . . '.

TABLE 1. Number of named species and open nomenclature forms of entomozoceans described from different stratigraphic divisions in the upper Devonian and Carboniferous. The divisions are: A, *Eumorphoceras* Stufe of ammonid chronology (Namurian A); B, *crenistrina* conodont zone (lower Tournaisian); C, *Pericycilus* Stufe (upper Tournaisian-lower Viséan); D, *latior* ostracod Zone (lower Tournaisian); E, upper *hemisphaerica-dichotoma* ostracod Zone (topmost Famennian).

Division	Entomozoe	Maternella	Richterina	Truyolsina	Bertillonella	Entomoprimitia	Ungerella
A	—	—	—	5*	—	—	—
B	—	1	—	—	—	—	—
C	—	4	6	—	—	1	1
D	—	16	5	—	3	—	4
E	2	6	4	—	—	1	—

* Including two subspecies.

In contrast to the plethora of entomozocean zones spanning the upper Devonian, only the *latior* Zone of Rabien (1960), which is broadly equivalent to the *Gattendorfia* Stufe of ammonoid chronology, is generally recognized within the Carboniferous. Rabien (1960) found that this zone was separated from the upper Devonian *hemisphaerica-dichotoma* Zone by a horizon characterized by a reduced number of entomozocean species and the abundant occurrence of *R. (R.) costata* and *R. (R.) striatula*. He termed this interval, which apparently includes the Devonian–Carboniferous boundary, the *hemisphaerica-latior* Interregnum. The most complete Carboniferous section with entomozoceans, and the only one actually spanning the lower boundary of the system, was exposed by trenching at Stockum in the Rheinische Schiefergebirge (Alberti *et al.* 1974; Groos-Uffenorde 1974). The ages of the ostracod-bearing layers in these trenches are accurately controlled by conodonts. The *hemisphaerica-dichotoma* Zone, the *hemisphaerica-latior* Interregnum, and the *latior* Zone can be recognized and an additional, hitherto undocumented, entomozocean fauna, comprising *M. (M.) circumcostata*, *M. (M.) n. sp. 3*, and *M. (S.) sp. 4*, is intercalated between the Interregnum and the *latior* Zone. *R. (R.) latior* itself, instead of persisting through most of CuI as it does in other parts of the Rheinische Schiefergebirge and in Thüringia, occurs only in the lower part of this division at Stockum. The upper part of CuI is characterized instead by the abundant occurrence of *M. (M.) cf. arcuata*, *M. (M.) clathrata*, and *M. (S.) schindewolfi*.

The proposed introduction by Becker and Bless (1974, p. 11) of a '*R. (R.) aff. latior-Zeit*', which is supposed to be equivalent to the middle-upper Tournaisian and part of the Viséan (approximately CuII, the *Pericycilus*-Stufe of ammonoid chronology), has been challenged by Groos-Uffenorde (in press) on the grounds that *R. (R.) aff. latior* includes several species, none of which is common. *M. (S.) geniceraensis* appears to be characteristic of most of CuII and has recently (Hauser, in Groos-Uffenorde, in press) been discovered in the lower part of CuIII (CuIIIa, the *crenistrina* Zone of conodont chronology = upper Viséan). However, it would be premature to establish a '*geniceraensis*-Zone' to succeed the *latior* Zone because entomozoceans have not yet been found at the base of CuII (Groos-Uffenorde, in press).

The last documented occurrence of *M. (S.) geniceraensis* is followed by an interval, corresponding to the topmost Viséan and basal Namurian, which has so far failed to yield entomozoceans. The youngest known representatives of the group occur in the basal upper Carboniferous (Namurian A) of northern Spain (Becker 1975, 1976) and are assigned to a distinct genus, *Truyolsina*.

I agree with the conclusion of Sanchez de Posada (1977, p. 72) and Groos-Uffenorde (in press) that although the Entomozoacea seem to be of stratigraphic use in some European lower Carboniferous strata, much work remains to be done.

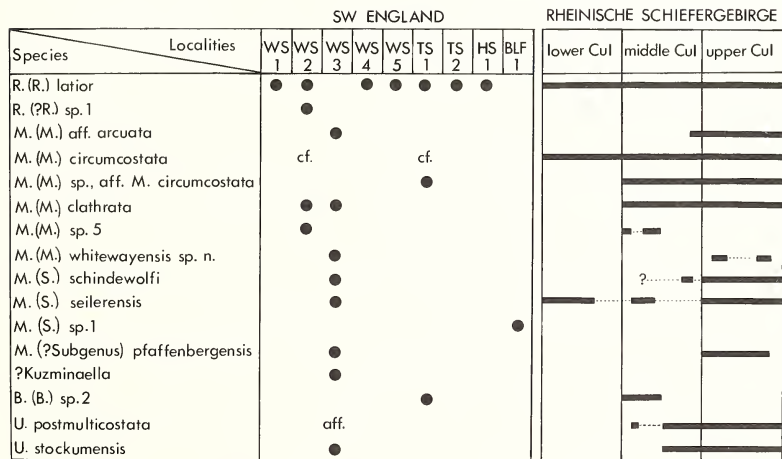
The British assemblages. The Entomozoacea described in this paper show a striking correspondence with the species recorded by Groos-Uffenorde (1974) from Stockum. With the exception of three rare forms—*R. (R.)* sp. 1, *M. (S.)* sp. 1, and ?*Kuzminaella* sp.—all the species which occur in Devon also occur at Stockum.

Text-fig. 12 summarizes the distribution of lower Carboniferous entomozoaceans among the nine British localities, together with the stratigraphic ranges given by Groos-Uffenorde (1974) for the same species in the Rheinische Schiefergebirge. On the basis of this comparison, the locality WS3 assemblage from the Whiteway Barton trench exposure can be confidently assigned to the upper *Gattendorfia* Stufe (Cul). The overlying strata with *R. (R.) latior* (localities WS4 and 5) presumably also belong to this division while a middle *Gattendorfia* Stufe age seems likely for the beds at locality WS2 in which there occur none of the species characteristic of the upper division. The presence of *B. (B.)* sp. 2 with *R. (R.) latior* at locality TS1 suggests that the middle part of Cul is also represented in the Trusham Shale.

The sparse entomozoacean fauna from the Hyner Shale includes only *R. (R.) latior* and hence is impossible to assign to any particular level within *Gattendorfia* Stufe. The age of the locality in the Bampton Limestone Formation which yielded *M. (S.)* sp. 1. is uncertain. However, the similarity of this species to *M. (M.)* sp. aff., *M. circumcostata*, and *M. (S.) geniceraensis* suggest that the upper part of the *Gattendorfia* Stufe, or perhaps the overlying *Pericyclus* Stufe, is represented here.

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TEXT-FIG. 12. Distribution of entomozoacean species in Devon and their stratigraphic ranges in the Rheinische Schiefergebirge according to Groos-Uffenorde (1974, tables 4, 5; in press, fig. 5).

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A HETEROPHYLLOUS CHEIROLEPIDIACEOUS CONIFER FROM THE CRETACEOUS OF EAST CHINA

by ZHOU ZHIYAN (CHOW TSEYAN)

ABSTRACT. *Suturovagina intermedia* Chow and Tsao (Cheirolepidiaceae) from the Cretaceous of China is redescribed and emended on the basis of abundant new material. Its leafy shoots are heterophyllous and show axillary branching. The juvenile shoots bear widely spaced scale leaves, while mature ones bear mainly broad leaves enclosing most or the whole of the stem, with either a gap or a suture between the two lateral edges. Leaves of different types of shoot are generally similar in cuticular structures. Their stomata differ from all other members of this family in the very elongated subsidiary cells which form a tube- to truncated cone-shaped projection. Some dispersed fossil secondary xylem of *Protopodocarpoxylon*-type proves to belong to the same plant. An associated male cone, *Classostrobus cathayanus* sp. nov. yielding *Classopollis* pollen is also referred to it. This is the largest male cone so far known from this family.

THE present paper contains a revised description of *Suturovagina intermedia* Chow and Tsao 1977, based on the abundant material collected in 1979 from Zhouchiawen, Qiya Town, in the eastern outskirts of Nanjing (Nanking) City, Jiangsu (Kiangsu) Province, East China. The plant-bearing formation consists mainly of greyish calcareous siltstones and fine-grained sandstones. It forms well-exposed but discontinuous outcrops on the south bank of the Yangtze River near Nanjing. The original type specimens of *S. intermedia* were collected from this same formation, though at a different locality (Shenglicun, Yanziji), some 15 km away from Qiya Town. The geological age of the formation has not yet been settled. Some consider that it may be correlated with the Gecun Formation in Jurong County, east of Qiya Town, which is regarded on palynological evidence (Zhang 1962) as being of lower Cretaceous age. No other fossils, however, have hitherto been found in the plant-bearing formation, nor has any detailed palynological work been done, which could confirm such a correlation. The plant megafossils described in this paper clearly indicate a Cretaceous age for the formation.

MATERIAL AND METHODS

S. intermedia is almost the only species of plant megafossil to have been found in this plant-bearing formation. Besides some large hand specimens with branched shoots or cones, thousands of fragments were obtained by bulk maceration of several kilograms of rock. The material consists of fragments of leafy shoots, secondary xylem, and male cones. Some small doubtful fragments of female organs have also been found, but they will not be described until better-preserved specimens are available. All the specimens described here have been deposited in the Institute of Geology and Palaeontology, Academia Sinica, Nanjing, China.

After bulk maceration in either HCl or HNO₃, the picked specimens were washed in HF to remove adhering sand grains. They were then examined with a binocular microscope and photographed dry or under paraffin. Most of the hand specimens were photographed under paraffin. The conventional maceration method using Schulze's solution was adopted for both compressed leaves and male cones. The compressed and fusainized fragments of secondary xylem were cut with a scalpel to expose fresh surfaces. All prepared specimens were examined and photographed with a Leitz Dialux 20 light microscope with an attached camera, or with a Super II ISI scanning electron microscope.

DESCRIPTIONS AND COMPARISONS

*Leafy shoot*Genus *Suturovagina* Chow and Tsao 1977

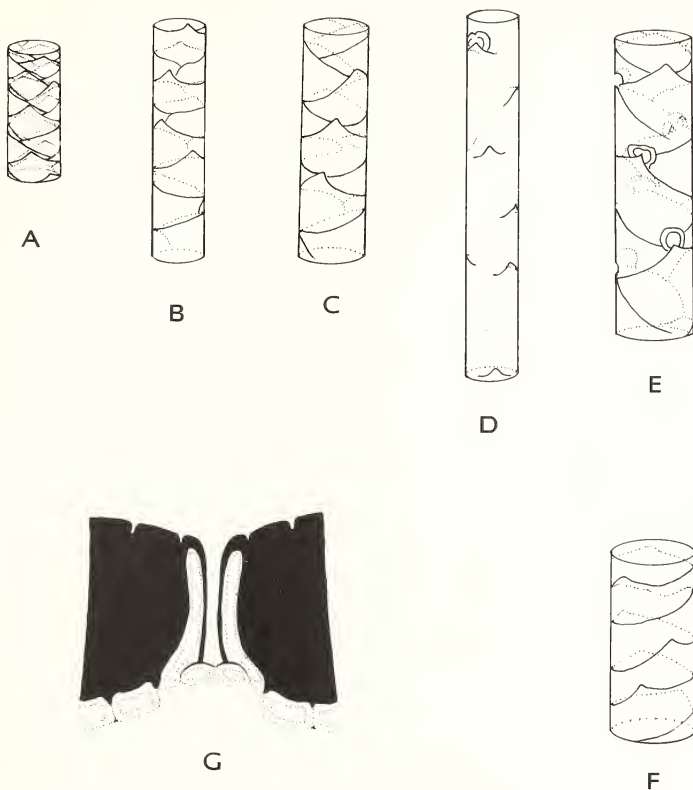
Type species. *S. intermedia* Chow and Tsao, 1977, p. 167.

Emended generic diagnosis. Plant with heterophyllous axillary branching shoots. Leaves persistent, adpressed, and spirally arranged; those on the juvenile shoot scale-like, and borne at intervals; those on the mature shoot, broad, scale-like, and imbricate, or more commonly slightly overlapping (occasionally separated), encircling most or all of the stem, leaving either a gap or a suture between the two lateral edges. Decurrent leaf base cushion crescentic, rhomboidal to short cylindrical with oblique ends. Stomata present on the abaxial cuticle, generally arranged in rows, actinocytic and monocyclic. Guard cells sunken at the bottom of a deep stomatal pit formed by vertical extension of the subsidiary cells. Subsidiary cells numerous.

Discussion. As implied by the specific name of the type species, *Suturovagina* is 'intermediate' in gross morphology of the leafy shoot between *Hirmeriella* (*Brachyphyllum* type) (Hörhammer 1933; Hirmer and Hörhammer 1934; Kendall 1947; Jung 1968; Harris 1979) and *Pseudofrenelopsis* (Nathorst 1893; Watson 1977). Both *Brachyphyllum*-type shoots with imbricate scale leaves and shoots with open-sheathed leaves, as in some *Pseudofrenelopsis*, are known to be present in *S. intermedia*. The *Brachyphyllum*-type shoot (text-figs. 1A, 2A, B, etc.), however, is not the prevailing one. It occurs probably only as the ultimate branchlet or the terminal portion of ultimate branchlets on the mature shoot. The shoot with open sheathed leaves (text-figs. 1B, C, E) is the predominant type in *Suturovagina*, while in *Pseudofrenelopsis* (Watson 1977; Alvin *et al.* 1978, p. 854) the shoot with close-sheathed leaves predominates. Though thousands of fragments have been examined, no typical shoot of *Pseudofrenelopsis* with close-sheathed leaves separated by long internodes was found. Only occasional shoots with complete-sheathed leaves in which the suture is very short and sometimes only represented by an inconspicuous notch, bear a resemblance to some of the shoots of *Pseudofrenelopsis*, though the leaves in such shoots are very short, and the length of the decurrent leaf base cushion (internode) rarely exceeds the breadth of the stem (text-fig. 2I). The shoot with scale leaves at intervals (shoot type 1; text-figs. 1D, 2E, F, G, H) is not known in any species of *Hirmeriella* or *Pseudofrenelopsis*, nor is the shoot with open-sheathed leaves which do not overlap, but are more or less separated from each other (Pl. 75, fig. 6), even though these two genera are abundant in some localities (e.g. *Pseudofrenelopsis* in the Isle of Wight). Theoretically, shoot type 1 could be derived from an ordinary shoot with imbricate scale leaves, by a very rapid acropetal growth of the apical meristem so that the primordia of leaves emerge at rather long plastochrons. Nevertheless, it appears to be a new type of leafy shoot for the Cheirolepidiaceae (Hirmerellaceae) as well as for the Coniferales.

The stomatal structure of *Suturovagina* (text-fig. 1G) is characteristic, and readily distinguishable from *Hirmeriella* (*Brachyphyllum*) and *Pseudofrenelopsis*. Nor do I know of any other conifer genus, living or fossil, with a similar stomatal structure. The great extension of the subsidiary cells is unique, though in many conifers hairs or papillae are not uncommonly seen on the periclinal walls of subsidiary cells.

Heterophylly has been reported in most genera of Cheirolepidiaceae. Some types of leafy shoots are, moreover, not restricted to any particular genus. The *Brachyphyllum*-type shoot seems to be an initial and rather common form. It is the dominant type in *Hirmeriella* (Harris 1979), and occurs in *Tomaxellia* (Archangelsky 1966), *Pseudofrenelopsis* (Watson 1977), and *Suturovagina*. The *Geinitzia*-type shoot is present in *H. crucis* (Kendall) as the juvenile shoot and becomes a predominant type of shoot in *Tomaxellia* (Harris 1979, p. 18; Archangelsky 1966, 1968). Decussate phyllotaxis characteristic of *Cupressinocladus* (Chaloner and Lorch 1960; Barnard and Miller 1976; Watson 1977) also exists in *H. crucis* (Harris 1979) and *Frenelopsis teixeirae* (Alvin and Pais 1978). The shoot with open-sheathed leaves predominant in *Suturovagina*, has been found in some species of



TEXT-FIG. 1. *Suturovagina intermedia* Chow and Tsao. A-F. Diagrammatical reconstructions of different types of shoots (all $\times 2$). A, *Brachyphyllum*-type shoot (based on PB 10184). B, shoot type 2 (based on PB 10223); C, shoot with open-sheathed leaves above and leaves with suture below (based on PB 10210); D, shoot with scale leaves at intervals (based on PB 10212); E, shoot with open-sheathed leaves, showing branchlet scars (based on PB 10200); F, abnormal shoot with 'continuing' leaves (based on PB 10180); G, reconstructed transverse section of a stoma as that in Pl. 78, fig. 10 (right), $\times 200$.

Pseudofrenelopsis (especially *P. varians* Fontaine; see Watson 1977). Thus, it is sometimes almost impossible to identify the genus when only a few isolated shoot fragments are available. I propose in the following key to separate the leafy shoots of different genera of Cheirolepidiaceae on the basis of the characters of their typical mature shoots.

- | | |
|--|--|
| 1. Phyllotaxis spiral | (2) |
| Phyllotaxis decussate or whorled | (6) |
| 2. Leaf for the most part free from the stem | (3) |
| Leaf adpressed | (4) |
| 3. Leaf somewhat dorsoventrally flattened | <i>Pagiophyllum</i> (<i>Hirmeriella</i>) |
| Leaf equally thick in vertical and horizontal directions | <i>Tomaxellia</i> , <i>Geinitzia</i> (? <i>Hirmeriella</i>) |
| 4. Leaf scale-like | <i>Brachyphyllum</i> (<i>Hirmeriella</i>) |
| Leaf encircling most or all of stem | (5) |
| 5. Leaf forming closed sheath | <i>Pseudofrenelopsis</i> |
| Leaf forming open sheath | <i>Suturovagina</i> |
| 6. Suture present between leaves | <i>Cupressinocladus</i> |
| Suture absent | <i>Frenelopsis</i> |

It is obvious that in some cases an accurate determination of leafy shoots, as well as their reference to the Cheirolepidiaceae, is possible only when cuticular structures and fructifications are known, especially those of *Hirmeriella*, *Tomaxellia*, and *Cupressinocladus* types.

Suturovagina intermedia Chow and Tsao

Pls. 75-77; Pl. 80, fig. 8; text-figs. 1A-G, 2A-J, 3A-C

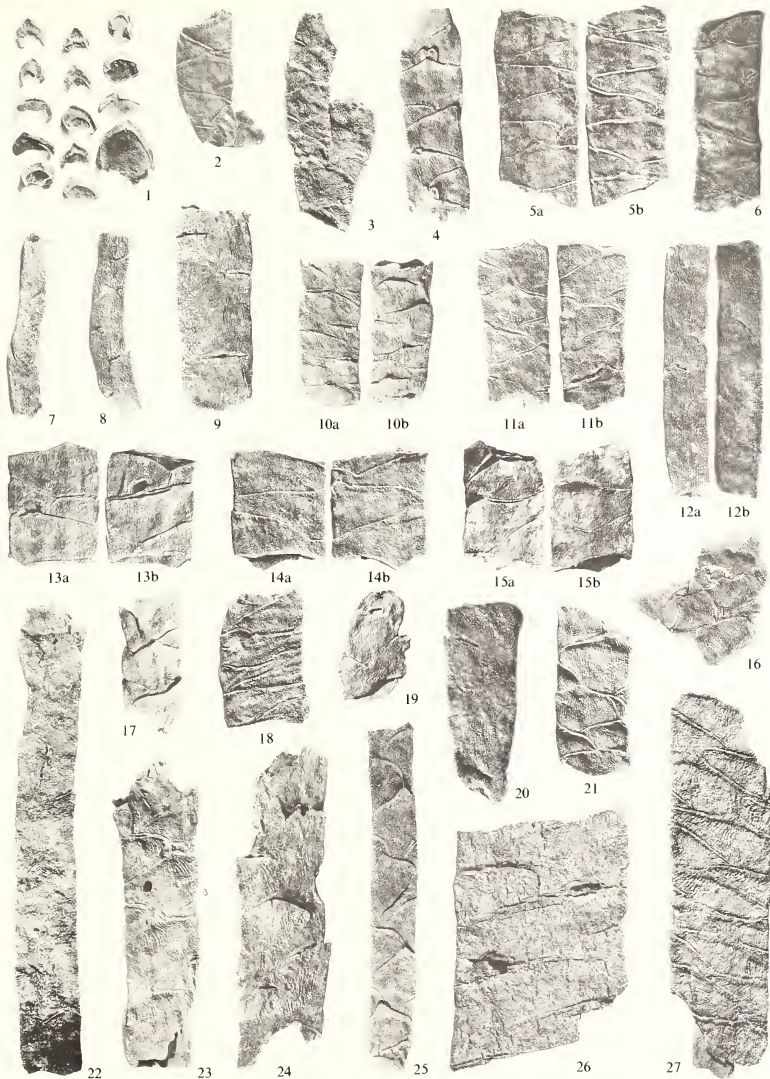
1977 *Suturovagina intermedia* Chow and Tsao, p. 167, pl. 2, figs. 1-14; text-fig. 1.

1979 *Suturovagina intermedia* Zhou and Cao, p. 220 (name only).

Emended diagnosis. Juvenile shoots bear irregularly spaced, very loose spirally arranged scale leaves. The slender mature shoots (ultimate branchlets) either have broad scale leaves (usually only seen at the terminal and basal portions of the shoot) or more commonly comparatively longer open-sheathed leaves with either a gap or a suture between the two lateral edges. The more robust mature

EXPLANATION OF PLATE 75

Figs. 1-27. *Suturovagina intermedia* Chow and Tsao; all figures are $\times 2$. 1, isolated scale leaves of different shape and size, PB 10185-10198. 2, a branchlet showing upward transition from scale leaf to open-sheathed leaf with either a gap or a suture between the two lateral edges, PB 10171. 3, a branchlet with scale leaves at the base and open-sheathed leaves above, PB 10175. 4, a shoot with open-sheathed leaves showing two axillary buds of branchlets, PB 10201. 5a, b, two sides of a shoot showing open-sheathed leaves with either a gap or a suture between the two lateral edges, PB 10224. 6, a shoot showing a gradual upward transition from open-sheathed leaf to leaf with sutured, complete sheath, PB 10204. 7, 8, 12a, b, ultimate juvenile shoots bearing scale leaves at long intervals, PB 10217, 10218, 10219. 9, a broad juvenile shoot with inconspicuous scale leaves, PB 10220. 10a, b, 11a, b, two sides of the juvenile shoots with large leaves at short intervals, PB 10176, 10182. 13a, b, two sides of a shoot showing two branchlet scars and leaves with either a suture or a notch, PB 10165. 14a, b, two sides of a shoot showing complete-sheathed leaves with a notch, PB 10209. 15a, b, two sides of a shoot with 'continuing' leaves, PB 10181. 16, a fragment of a shoot with two successive branchlets, PB 10216. 17, a shoot showing imbricate leaves, some of them merging into the adjacent ones, PB 10178. 18, 23, 25-27, shoots of different dimensions with open-sheathed leaves. Note the longitudinal fissures on the cuticle of the broadest shoot in 26 and buds and scars of branchlets here and there, PB 10168, 10172, 10206, 10169, 10222. 19, apical part of a juvenile shoot showing short intervals between leaves, PB 10163. 20, branchlet showing the leaf interval becoming shorter towards the contracted basal part, PB 10213. 21, a shoot showing an abnormal suture on one of the open-sheathed leaves, PB 10177. 22, a juvenile shoot with ten leaves, only seven visible in the figure, PB 10202. 24, a broad juvenile shoot with large leaves at short intervals, PB 10167.



ones (main branchlets or branchlets of lower order) have comparatively short, open-sheathed leaves usually with a wide gap between the two lateral edges. Leaves with only the small, apical portion free, normally arranged in 2/5 (occasionally 3/7–3/8) loose spiral phyllotaxis. Leaf apex broadly acute, 90–120°. Adaxial side of leaves triangular to almost ring-shaped, usually short or undeveloped, but may reach three-quarters (or even equal) the length of some small scale leaves of the mature shoot. Abaxial side decurrent, with numerous roughly parallel grooves tending to converge towards the apex. Leaf upper margin entire, sometimes scarious and microscopically dentate, especially on the juvenile shoots. Cuticles of leaf very thick. Adaxial side composed mainly of elongated cells. 40–110 × 20–70 μm , arranged in longitudinal rows tending to converge towards the apex. Abaxial side up to 250 μm thick, with sunken stomata in the grooves, arranged in roughly longitudinal uniseriate files (sometimes biseriate at the lower part of leaf and more or less irregular on juvenile leaf); apex, margin, and base of leaf usually free from stomata. Juvenile shoot leaf base stomatiferous, merging uninterruptedly into the stem. Stomata elliptical to rounded in surface view, 40–150 × 30–100 μm in diameter; guard cells 50–80 × 15–30 μm ; apertures randomly orientated. Subsidiary cells normally eight (range six to eleven) in number, of nearly uniform shape and size, round to elliptical in surface view and 10–30 μm in diameter, projecting upwards, up to 200 μm high, surrounding the stomatal pits, without a conspicuous papilla or hair on the periclinal wall. Encircling cells absent. Epidermal cells adjacent to stomata, usually differing slightly from the rest in shape and size. Epidermal cells normally larger than subsidiary cells in surface view, 10–60 × 7–65 μm , rectangular to polygonal, arranged in one to three longitudinal rows between each row of stomata. The epidermal cells in the stomatal rows are usually smaller and more irregular in shape. Anticlinal walls of cells straight. Periclinal walls smooth or sometimes slightly bulging. Compressed secondary xylem core one-third to two-thirds total width of shoot. Tracheids 7–12 μm in diameter, with crowded to sparse, uniseriate, elliptical to nearly round bordered pits, 6–8 × 4–6 μm on the radial surface.

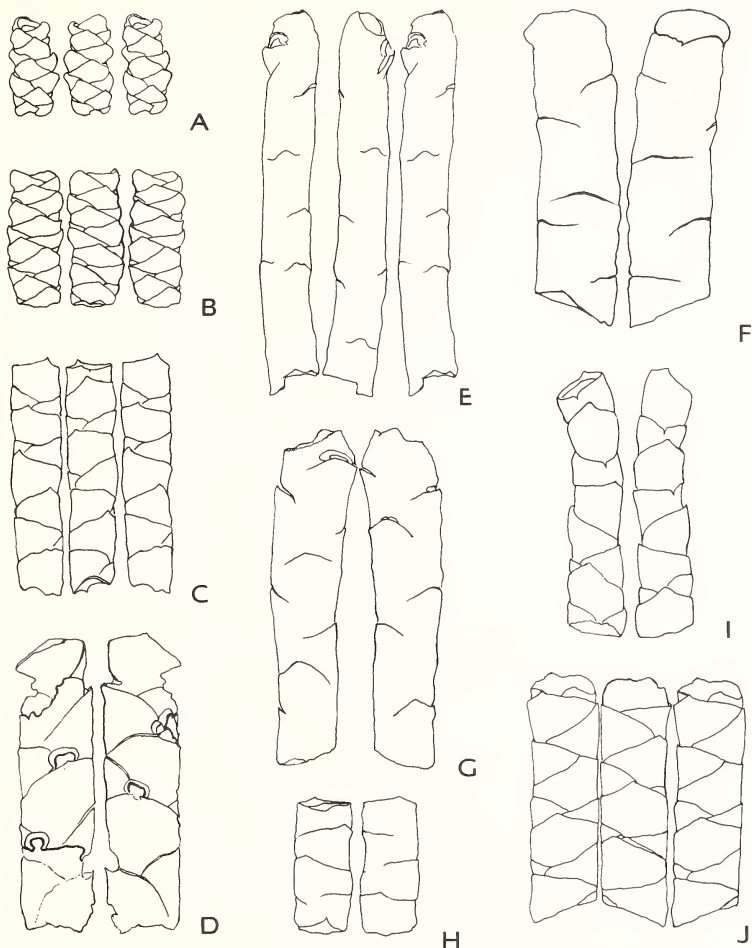
Description and discussion. The longest shoot seen is 165 mm long and incomplete. The most slender one is only 2 mm wide, while the widest reaches 20 mm. They vary considerably in having leaves of different shapes. Three main types of shoot were recognized:

1. Shoot bearing very loose spirally arranged scale leaves at intervals (text-fig. 1D).
2. Shoot bearing leaves encircling the stem with a complete sheath which is usually interrupted by a distinct suture (text-fig. 1B).
3. Shoot covered with broad scale-like to open-sheathed leaves (text-fig. 1A, E).

The longest shoot of type 1 so far obtained has ten leaves and is 47 mm long (Pl. 76, fig. 8). The leaves are small, triangular to crescent-shaped, with scarious margins. Their adaxial surface is usually of less than half the height of leaves and becomes indiscernible on the wide shoots. The interval between each two adjacent leaves (namely the vertical distance from the apex of a leaf to the base of the leaf above) varies according to their position on the shoot and the width of shoot on which they were borne. Normally, the interval between two leaves tends to shorten towards both ends of a shoot and the longer intervals occur in connection with the narrower shoots, but irregular intervals are sometimes present on the same shoot (text-fig. 2E).

Type 2 is represented in the material by comparatively fewer shoots which are of medium width (text-figs. 2C, I; Pl. 75, figs. 13a, b, 14a, b), no shoots being found less than 3.5 mm or more than 9 mm in diameter. The leaves are broad and encircle the axis laterally to form a complete sheath. A distinct suture is usually seen below a notch in the leaf margin. The adaxial side of the leaf is short and somewhat ring-shaped. The abaxial side is decurrent and normally slightly overlapped by the apical portion of the leaf below. The decurrent leaf base cushion is cylindrical with oblique ends. Normally, the height of the exposed part of a leaf matches the width of the shoot, but a slender shoot usually bears higher (longer) leaves and a broader shoot, shorter leaves.

The most common shoots in the debris belong to type 3. They display certain variations in the width of shoot as well as the shape of leaves. Slender shoots (3–6 mm; text-fig. 2A, B) usually bear



TEXT-FIG. 2. *Suturovagina intermedia* Chow and Tsao (all are $\times 2$, showing both sides of compressed shoots; one side of the shoot is sometimes drawn twice in order to show the continuity of leaves on the two sides clearly). A, B, *Brachyphyllum*-type shoots belonging to the terminal portion of ultimate branchlet, PB 10183, 10184; C, shoot showing leaves with complete sheath interrupted by a suture, PB 10223; D, shoot with open-sheathed leaves and about six consecutive branchlet scars, PB 10200; E-H, shoots with scale leaves at intervals; E, G showing scars or buds of branchlets, PB 10212, 10221, 10199, 10207; I, most leaves having an inconspicuous notch-like suture, except for the basal two leaves which have a wide gap between the two lateral edges, PB 10211; J, the five leaves on the upper part of a shoot with an incomplete open-sheath, those on the lower part with a complete sheath interrupted by a suture, PB 10210.

broad scale-like imbricate leaves which encircle more than half the width of the stem. Stout shoots (4–20 mm; text-fig. 1D, J; Pl. 75, figs. 18, 23, 25–27) commonly bear overlapping open-sheathed leaves which enclose the large portion of the stem, leaving a gap between the two lateral edges. There exists, however, no line of demarcation between them. The adaxial surface of leaves is well developed and triangular to crescentic in shape. The leaf base cushions vary from crescentic to rhomboidal. The basal part of the abaxial surface of the leaf is often concealed. On some shoots the open-sheathed leaves are separated from each other, as the basal part of the leaf abaxial surface is exposed and merges into the stem (Pl. 75, fig. 6). Normally, the height (length) of a leaf is more or less equal to the width of the shoot on which the leaf was borne, but leaves are longer on a slender shoot and shorter on a robust shoot.

There is a series of transitional forms between shoots of type 2 and type 3 as well as those of type 3 and type 1. On a shoot of type 2, there may occur leaves with their two lateral edges nearly attached or separated by a narrow gap (text-fig. 2i; Pl. 75, fig. 5a, b). The reverse is the case in some shoots of type 3 (text-fig. 2j; Pl. 75, figs. 4, 6). These shoots, in fact, could be referred to either type 2 or type 3 with equal justification. In some shoots of type 1 (Pl. 75, figs. 10a, b, 11a, b, 24), the intervals between leaves tend to be shortened and the scale leaves become large and arranged in closer spiral. Such shoots come very near to some of the shoots of type 3 on which the leaves do not overlap but are separated from each other by intervals (Pl. 75, fig. 6). Although there are no direct links between shoots of type 1 and type 2, various shoots of type 3 could fill the morphological gap.

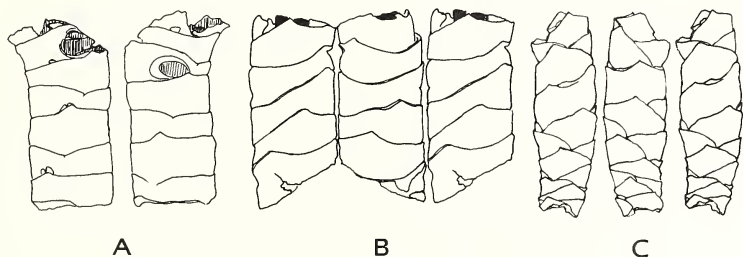
A few extremely unusual shoots (text-figs. 1f, 3b; Pl. 75, fig. 15a, b) were found in the debris after a careful search among thousands of specimens. They look as if they are 'segmented' as in *Frenelopsis* and *Pseudofrenelopsis*, but after close examination, I found surprisingly that the upper edges of leaves are continuous with those of the adjacent leaves above and below, to form a spiral line encircling the

TABLE 1. Measurement of different types of shoots; values for the gross morphological data are based upon at least fifty measurements.

	Shoot with scale leaves at intervals	Shoot bearing complete sheathed leaves with a suture	Shoot with open-sheathed leaves	Shoot with imbricate scale leaves
Length of leaves	0.5–2 mm $m = 1.06 \text{ mm}$, $\sigma = 0.43$	3–9 mm $m = 4.92 \text{ mm}$, $\sigma = 1.39$	2.5–10 mm $m = 5.3 \text{ mm}$, $\sigma = 1.62$	2–6 mm $m = 3 \text{ mm}$, $\sigma = 0.98$
Breadth of shoots	2–15 mm $m = 5.3 \text{ mm}$, $\sigma = 2.45$	3.5–9 mm $m = 5.16 \text{ mm}$, $\sigma = 1.57$	4–20 mm $m = 6 \text{ mm}$, $\sigma = 3.38$	3–6 mm $m = 4.26 \text{ mm}$, $\sigma = 0.84$
Interval between leaves	1–15 mm (occasionally leaves overlap)	Leaves slightly overlap		Leaves overlap
Ratio of length of leaf to width of shoot	One-thirtieth to two-thirds	Half to one and three-quarters	Half to two	Half to two
Size of stomata (outside view)	75–100 × 40–60 μm (On robust shoot 40–50 μm in diameter)	50–80 × 40–60 μm	40–70 × 25–30 μm (On robust shoot 100–120 μm × 60–80 μm)	40–100 × 40–65 μm
Size of stomata (inside view)	90–125 × 60–100 μm (On robust shoot 100–180 × 70–100 μm)	50–100 × 30–60 μm	40–100 × 40–60 μm (On robust shoot 80–120 × 50–100 μm)	50–100 × 60–80 μm
Density of stomata	24–36/mm ² (On robust shoot 16–20/mm ²)	40–50/mm ²	32–56/mm ² (On robust shoot 14–20/mm ² inside view, 4–7/mm ² outside view)	64–130/mm ²
Size of epidermal cells	15–60 × 30–65 μm	15–60 × 30–60 μm	10–40 × 15–70 μm	7–30 × 10–40 μm

stem. Perhaps such a kind of shoot is an abnormal variant, as specimens are very rare, only two fragments being so far found. On rare shoots of type 3 (text-fig. 3c; Pl. 75, fig. 17), there are a few leaves which tend to merge into the adjacent ones by a shortening or vanishing of lateral edges.

The great variation in leafy shoots, which we encountered in the material, suggests that we are dealing with a heterophyllous conifer. Shoots of type 3 have a great range in width, and are therefore thought to represent shoots on different positions of the plant. The most slender ones have the usual *Brachyphyllum* aspect. No branched specimens of this kind have been found. Presumably, they represent the ultimate branchlets or the terminal portions of the ultimate branchlets. The broadest shoot of type 3 so far found in the debris attains 20 mm in breadth; it is characterized by short open-sheathed leaves covered with very tough cuticle. The leaves usually have conspicuous longitudinal fissures on their surface (Pl. 75, fig. 26; Pl. 76, fig. 7), which suggest a tangential expansion of the shoot due to subsequent growth. I believe, therefore, that such robust shoots with short leaves represent the main branchlets. There are transitional forms of which the shoots and leaves are intermediate in thickness and shape respectively between the two extremes. Those slender shoots with longer leaves are considered to be ultimate or penultimate branchlets, while those broader shoots with shorter leaves are thought to belong to branchlets of lower order.



TEXT-FIG. 3. *Sutyrovagina intermedia* Chow and Tsao (all are $\times 2$; both sides of the compressed shoots are shown, one side of shoots in B and C being drawn twice). A, a shoot with scars and buds of branchlets, PB 10170; B, an abnormal shoot with 'continuing' leaves and a compressed xylem core, PB 10180; C, a shoot with imbricate scale leaves bearing some abnormal 'continuing' leaves in the middle part, PB 10179.

Shoots of type 2 are few in number and have a rather limited width range in comparison with those of type 3. It seems that type 2 has not been an important variant of the shoot on the plant but occurs mixed with type 3 on certain branchlets (most probably penultimate ones). No shoots which could be regarded as ultimate or main branchlets have been found.

Like type 3, type 1 has a complete series of shoots of its own (Pl. 75, figs. 7-12b, 20, 22) which cover a range of width of 2-15 mm. Although there are intermediate forms between types 1 and 3, their typical forms never seem to occur on the same branch. Since type 1 includes the most slender shoots with the longest leaf interval and since these shoots are scarcely branched and have leaves with thinner cutinized cell walls compared with those of similar width of other types, I am inclined to regard type 1 as the shoot of the juvenile tree or the newly formed shoot of the mature tree, such as in some extant conifers (e.g. *Juniperus chinensis* L.). It is also worth mentioning that, on the surfaces of leaves of the broadest specimen of type 1, longitudinal fissures like those of the broadest mature shoot do not exist.

Despite the great variation in gross morphology of shoots, the cuticular structures of leaves are essentially similar. The variation in details of the cuticle is mainly associated with the age of shoots and the state of preservation. The outlines of epidermal cells are more clearly seen on the inner side of

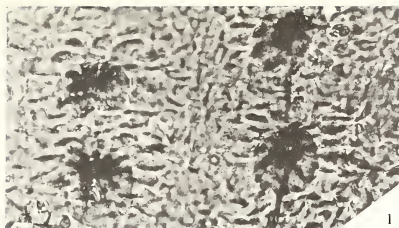
the leaf cuticle. In outside view, they are often obscure, especially in juvenile and old shoots, which might be due partly to presence of the outermost wax layer. Their periclinal walls are normally more or less bulging and smooth in surface view, but occasionally have a papilla (Pl. 77, fig. 5). The anticlinal walls are thin ($1-3\text{ }\mu\text{m}$ wide) in leaves of most juvenile shoots, but much thicker (commonly $5-10\text{ }\mu\text{m}$ wide) in leaves of mature shoots. In the leaves of robust juvenile shoots, the anticlinal walls of cells are also thickened and the lumina of cells are very narrow (Pl. 76, fig. 5). The size of epidermal cells and stomata normally decreases in leaves of mature and robust shoots. The density of stomata, however, which varies to a certain extent within a single leaf (higher in lower part where stomata are biseriate), tends to be higher in most mature shoots, though lower in robust shoots (Table 1). Leaves of old and robust shoots with tough cuticle often have very sparse stomata on the outer surface because of the presence of longitudinal fissures between files of stomata (Pl. 76, fig. 7), though stomata are more frequent on the inner surface of the cuticle. Hypodermal cells have not been seen on leaf cuticles except some possible traces of cell wall on some cuticle of certain juvenile shoots (Pl. 77, fig. 8).

The most characteristic feature of the cuticles is the structure of the stomata, which remains unchanged on leaves of all types of shoots. Most of the stomata examined have lost their guard cells. More or less well-preserved guard cells were only seen on leaves of the juvenile shoots. The distal walls of subsidiary cells are as a rule strongly cutinized, while the radial and proximal walls were not preserved on most of the leaves studied.

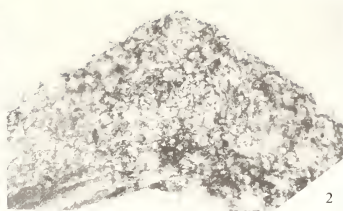
Branched shoots are not common in the debris. This may be partly due to the maceration which dismembered the shoots. In hand specimens, shoots longer than $10-15\text{ cm}$ are not uncommon, but again most of them are unbranched. Almost all the branched shoots studied are more than 4 mm wide. They show normal axillary branching like that in *Pseudofrenelopsis parceramosa* (Watson 1977, Pl. 85, fig. 3; Alvin and Hlůstík 1979, pp. 239-240, text-fig. 15), but no whorled branching such as that observed by Alvin in *P. parceramosa* (pers. comm.) has been seen. The branchlets arise immediately above the subtending leaves on the parent shoot. Initially, a pair of small leaves emerges (Pl. 75, figs. 4, 23; text-figs. 2G, 3A), which are of about the same size and laterally symmetrical to each other, though occasionally asymmetrical. Sometimes there may be one or three leaves instead of two. These two leaves which cover the base of the branchlet afterwards (Pl. 75, fig. 3), are always shorter and smaller than the succeeding leaves on the branchlet and are of the same shape on different types of shoots. The branchlets (or branchlet scars and buds) which always contract at the bases, are carried at rather irregular intervals on the shoots. One shoot (text-fig. 2D) has been found to have at least six successive, spirally arranged branchlet scars, but others show branching intervals of one to many (up to more than twenty) leaves. When branched sparsely, the shoot often shows an appearance of alternate branching in one plane (Pl. 80, fig. 8). As there are no specimens which are large enough to show the whole branching system, it is almost impossible to ascertain whether different intervals of branching occur on the same shoot or not. It appears, however, that this is likely, as the leaves are

EXPLANATION OF PLATE 76

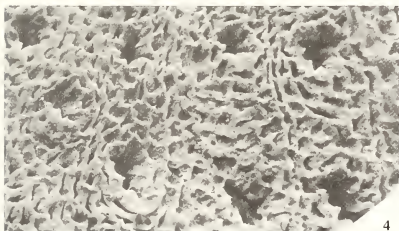
Figs. 1-8. *Suturovagina intermedia* Chow and Tsao; all are SEM photographs except 1 and 2. 1, abaxial cuticle showing cone-shaped stomata, $\times 135$. PB 10225. 2, adaxial cuticle of an open-sheathed leaf, $\times 30$. PB 10226. 3, outer surface of the apical portion of the abaxial cuticle of an open-sheathed leaf, showing rather thick and smooth margin, $\times 100$. PB 10231. 4, inner surface of an abaxial cuticle (open-sheathed leaf), no guard cells being preserved, $\times 200$. PB 10234. 5, inner surface of the stem cuticle from a robust juvenile shoot, showing thick anticlinal walls and narrow lumen of cells, $\times 200$. PB 10235. 6, inner surface of the stem cuticle from a juvenile shoot, showing thin anticlinal walls and large lumen of cells, $\times 200$. PB 10233. 7, outer surface of a leaf cuticle (robust mature shoot of type 3) showing sparse stomata and longitudinal fissures between stomatal files, $\times 50$. PB 10240. 8, outer surface of the abaxial cuticle of a leaf (*Brachyphyllum*-type), $\times 100$. PB 10229.



1



2



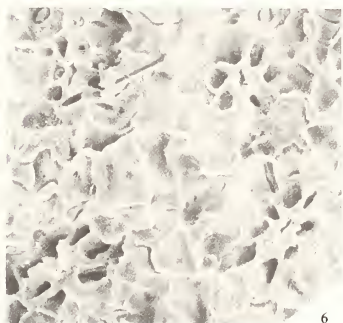
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3



5



6



7



8

sometimes also carried at very different intervals on the same shoot (text-fig. 2e). The branched shoots which are of very different thickness and with different ratios of leaf height to width of shoot, may suggest a fairly complicated, repeated branching. Perhaps, *Suturovagina intermedia* had a branching system similar to that of *Frenelopsis ramosissima* Fontaine (Fontaine 1889, Pls. 95–100; Watson 1977, Pls. 93, 94), although branching was far more sparse, especially in the juvenile shoot.

Little is known about the structures of the compressed xylem core of the shoots, as many specimens studied are structureless. Only a few show outlines of tracheids on the transverse and radial sections, and one, belonging to a 17 mm broad leafy shoot, shows bordered pits on the radial walls of tracheids (Pl. 78, fig. 5). No elements other than tracheids have been identified, though traces of ray cell walls have been seen on the radial fractures of some specimens.

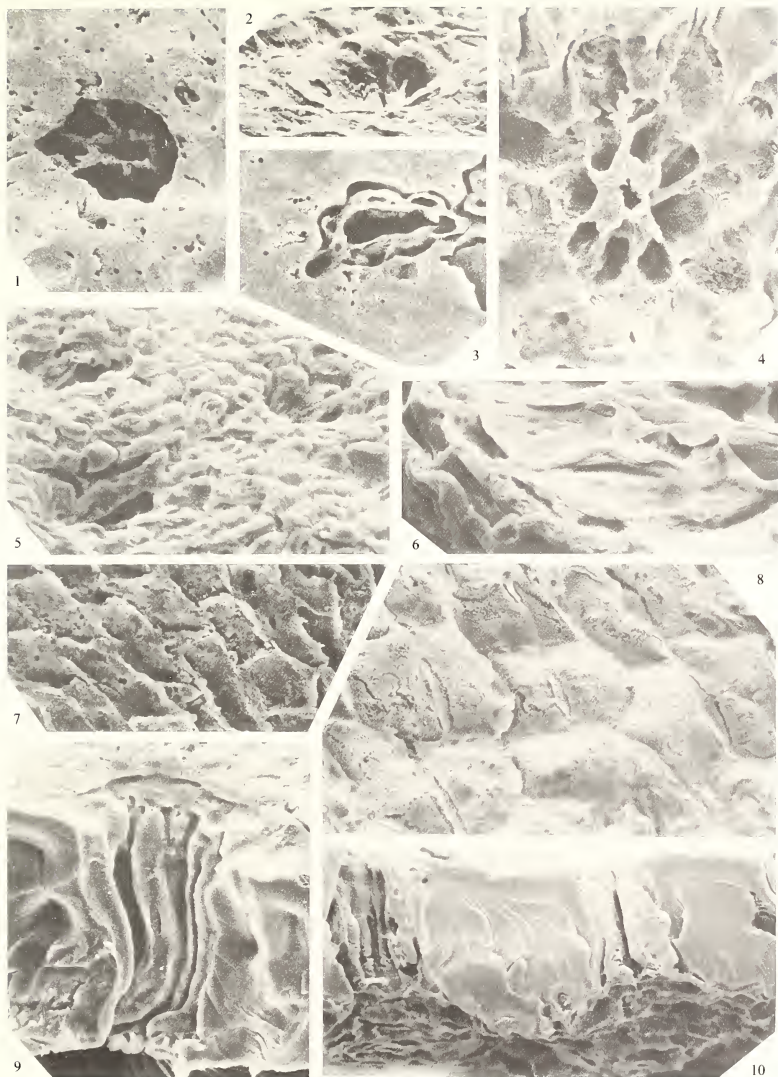
Comparison. In addition to the type-species, there are at least two other forms described from different formations of China as *Brachyphyllum obtusum* and *Manica tholistoma* (Chow and Tsao 1977; Zhou and Cao 1979), which should perhaps be referred to *Suturovagina*. Both are similar to *S. intermedia* in many respects, especially in stomatal structures, but they are different in some details. *B. obtusum* is represented by a single *Brachyphyllum*-type shoot which is, however, distinguished by having obtuse leaves, a feature not known in any shoots from the present abundant material. The adaxial cuticle is also characteristic as the epidermal cells are smaller and more or less isodiametric. All the shoots referred to *M. tholistoma* look like those of *S. intermedia* with complete-sheathed leaves without a suture (Pl. 75, figs. 14a, b), but the type specimen of *M. tholistoma* (Chow and Tsao 1977, Pl. 5, figs. 1–2) shows more marked surface grooves and larger, more crowded stomata in comparison with the mature shoots of *S. intermedia*. It is not certain whether the two forms (especially *M. tholistoma*) actually represent distinct species, because some of the differences are of little taxonomic importance, particularly if we take the great variation of cheirolepidiaceae conifers into consideration. As no other types of shoot nor the variation of cuticular structures are known, a closer comparison and further discussion are at present impossible. I would keep them separate from *S. intermedia* for the time being until more specimens are available for examination.

Secondary xylem

Associated fusainized and compressed wood specimens have been studied under SEM and the light microscope. Two different forms of secondary xylem have been recognized, chiefly based on the information obtained from fusain. Both are composed of tracheids with parenchymatous rays. One form, characterized by spiral thickening(?) in tracheids and one to two superimposed large bordered pits in the cross field, was regarded as representing a gymnosperm of a quite different taxon. Another form has been considered to belong to *S. intermedia* and is described below. The evidence of attribution of this dispersed secondary xylem consists in the close association with leafy shoots and in the similarity in tracheids to the compressed xylem of some corticated leafy shoots. (Cf. Pl. 78, figs. 4,

EXPLANATION OF PLATE 77

Figs. 1–10. *Suturovagina intermedia* Chow and Tsao; all are SEM photographs. 1, outside view of a stoma from the cuticle of a robust juvenile shoot, $\times 400$. PB 10235. 2, outside view of a stoma from a leaf of shoot type 2, $\times 400$. PB 10230. 3, outside view of a stoma from a juvenile shoot, outlines of epidermal cells not seen, $\times 400$. PB 10218. 4, inside view of a stoma showing hollow subsidiary cells which are smaller than the normal epidermal cells, $\times 400$. PB 10233. 5, outer surface of an adaxial cuticle showing papillae on some epidermal periclinal walls, $\times 400$. PB 10232. 6, stoma in inside view, showing the guard cells, $\times 700$. PB 10228. 7, adaxial side view of an adaxial cuticle, $\times 400$. PB 10241. 8, possible trace of hypodermal cell walls seen on the inner surface of a stem cuticle from a juvenile shoot, $\times 400$. PB 10233. 9, a stoma in transverse section (from the leaf on a *Brachyphyllum*-type shoot) showing the vertical extension of subsidiary cells and the more or less funnel-shaped upper part of stoma, $\times 400$. PB 10229. 10, transverse section of stomata (from a juvenile leaf) showing the guard cells deeply sunken at the bottom of the stomatal pits, $\times 200$. PB 10228.



ZHOU, cheirolepidiaceous conifer

8 with Pl. 78, fig. 5.) In the debris obtained, about 95% of fossil fragments are of *Suturovagina*, and no other macrofossils are known to have comparable tracheids. The close resemblance in structure between the present secondary xylem and the secondary xylem already proved to belong to other Cheirolepidiacous conifers (see below) also supports the attribution.

Description. Transverse section (Pl. 78, figs. 1, 3): the secondary xylem is compact and consists of tracheids and parenchymatous rays only. The growth rings are distinct and of various widths from 150 to 850 μm . The early wood is formed by a broader zone of tracheids with larger lumina. The late wood is composed of a narrower zone (four to six cells only) of tracheids with narrower lumina. In cross-section, the tracheids are rectangular to polygonal, $10\text{--}26 \times 8\text{--}30 \mu\text{m}$ in the early wood and $5\text{--}10 \times 15\text{--}25 \mu\text{m}$ in the late wood. Their walls vary from 1 to 7 μm in thickness. There are about 2,000–3,000 tracheids per square millimetre in the early wood. The septate tracheids are present occasionally in the late wood. No resin ducts or cysts have been detected.

Tangential section (Pl. 78, fig. 2): the tangential surfaces of tracheids are only rarely pitted. Pits are small (about 10 μm in diameter), bordered, and form short, contiguous single rows. The parenchymatous rays are overwhelmingly uniseriate and low, one to nine (mostly less than four to five) cells high. There are about forty-five to eighty rays per square millimetre. The ray cells are usually slightly elongate, about $12\text{--}30 \times 10\text{--}20 \mu\text{m}$ in size, with thin horizontal walls.

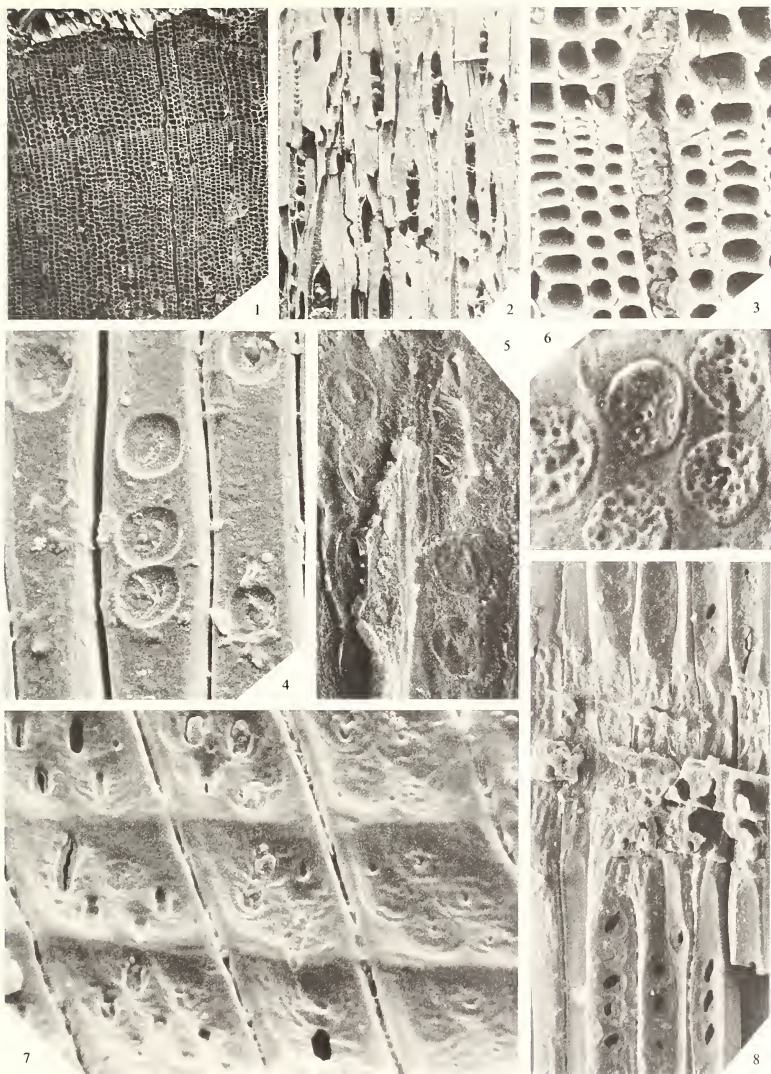
Radial section (Pl. 78, figs. 4, 6–8; Pl. 79, figs. 1–2): the bordered pits are arranged in single, contiguous or sparse rows on the radial walls of tracheids, but sometimes, the tracheids are not pitted for the large part. Pits are 10–15 μm in diameter, with an elliptical to almost rounded aperture, $5\text{--}8 \times 2\text{--}5\text{--}4\text{--}0 \mu\text{m}$ in size. The rays consist entirely of parenchymatous cells with thin and smooth transverse and tangential walls. No pitting is seen on the horizontal and tangential walls. The cross fields are rectangular, $12\text{--}22 \times 10\text{--}25 \mu\text{m}$, either vertically or more often transversely elongated. There are normally four to six (range two to eight) cupressoid pits arranged in one to three horizontal rows in each field, which are broadly elliptical to rounded in outline, $4\text{--}6 \times 3\text{--}5\text{--}6\text{--}0 \mu\text{m}$ in size, separated from each other or slightly contiguous. The apertures are elliptical, $2\text{--}5\text{--}4\text{--}0 \times 1\text{--}5\text{--}2\text{--}0 \mu\text{m}$ and obliquely orientated in the same direction. No vertical wood parenchyma has been found, nor any trace of resinous tracheids.

Remarks. The above description was based on several well-preserved small pieces of fusain of twigs, the largest of which is estimated at 2 cm in diameter (partly shown in Pl. 78, fig. 1). Many slender dispersed compressed wood cores (most of them, in fact, being decorticated shoots) have also been studied, and proved to be essentially similar in structure. They have a similar number of cupressoid pits in the cross field. The secondary xylem pitting is of the same 'mixed' type, though alternative biseriate bordered pits sometimes occur. These are, however, not figured because the material was not so well preserved as the fusain.

On the transverse section of the late wood, horizontal cross walls are seen on occasional tracheids which have been, therefore, interpreted as septate. However, I failed to prove the existence of septate tracheids on the radial and tangential sections.

EXPLANATION OF PLATE 78

Figs. 1–8. Secondary xylem; all are SEM photographs and from PB 10242, unless otherwise stated. 1, transverse section, showing irregular growth rings, $\times 50$. 2, tangential fracture, showing the low rays and pitting on some tracheids (upper left), $\times 100$. PB 10243. 3, as 1, showing the transverse walls in a few tracheids of the late wood and amorphous deposit in the ray cells, $\times 400$. 4, radial surfaces of tracheids showing either sparse or crowded bordered pits, $\times 1000$. 5, radial fracture of the *in situ* compressed secondary xylem from PB 10169, showing pitting on tracheids, $\times 2000$. 6, pits of 'vestured' appearance in a cross field, $\times 5000$. 7, cross fields with crowded cupressoid pits, $\times 2000$. 8, radial fracture showing ray cells, cross fields, and tracheids with bordered pits, $\times 400$. PB 10243.



The ray cells are usually represented by cavities separated by thin transverse walls on the tangential section. Occasionally, they are filled with amorphous material (resin?). They are probably uniseriate throughout. Some wide gaps shown on the tangential surface suggest possible biseriate rows in the middle of rays, but they may represent distended or distorted ones formed by charring (Harris 1957, pp. 295–296).

The pits in the cross fields normally have smooth and flat borders, but pits of a 'vestured' appearance are also occasionally present (Pl. 78, fig. 6).

The presence of uneven growth rings, which occur usually in traumatic wood, is of interest as it is not inconsistent with the irregular intervals between leaves (and probably branchlets too) on some shoots of *Suturovagina*. A similar phenomenon has also been noticed by Alvin *et al.* (1981) on *Pseudofrenelopsis parceramosa*. They believed that it may well be related to periods of drought when growth was interrupted.

The similarity in structure between tracheids of the dispersed fragments of fusain described above and those of the compressed corticated shoots has already been mentioned. The only difference known is the smaller size of bordered pits and tracheids in the compressed woods. This, however, might be expected between a slender and a broader twig.

Comparison. I can find no important differences between the specimens of secondary xylem under discussion and those of some other members of Cheirolepidiaceae. All of them belong to *Protopodocarpoxylon* or *Protocupressinoxylon* which are characterized by 'mixed' pitting on the tracheids, parenchymatous rays, and podocarpoid to cupressoid pits in the cross field.

The secondary xylem of material from the Rhaeto-Liassic of South Wales, referred by Harris (1957) to *Cheirolepis* (= *Hirmeriella*) *münsteri*, has similar pitting on the tracheids and similar rays (one to eight cells high), but the growth rings are inconspicuous and the cross fields which contain a similar number (three to eight) of pits are usually longitudinally elongated.

Protopodocarpoxylon aveiroense Lauverjat and Pons 1978, a secondary wood from the Senonian of Portugal that is believed to belong to *Frenelopsis oligostomata* Romariz, differs only in detail from the present form. The growth rings are distinct but the late wood is narrow and inconspicuous. The tracheids are larger so that there are less tracheids (830–1,450) per square millimetre in the transverse

TABLE 2. Comparisons between secondary xylems referred to different members of Cheirolepidiaceae.

	<i>Hirmeriella münsteri</i> (from S. Wales)	<i>Frenelopsis oligostomata</i> (<i>Protopodocarpoxylon</i> <i>aveiroense</i>)	<i>Pseudofrenelopsis</i> <i>parceramosa</i>	<i>Suturovagina intermedia</i>
Growth ring	Inconspicuous	Present	Distinct but uneven	Distinct but uneven
Number of tracheids per mm ² in transverse section	—	About 830–1,450	About 520 (silicified specimen), 1,250 (fusain)	About 2,000–3,000 (fusain)
Pitting of tracheid	'Mixed' type	'Mixed' type	'Mixed' type	'Mixed' type
Septate tracheid	Unknown	Absent	Present	Present
Resinous tracheid	Unknown	Present	Present	Unknown
Shape of cross field	Square to longi- tudinally elongated	Longitudinally or hori- zontally elongated	Square to slightly elongated horizontally	Longitudinally or hori- zontally elongated
Number of pits per cross field	About 4 (range 3–8)	1–13	4–10 (range 1–17)	4–6 (range 2–8)
Parenchymatous ray	Probably all uni- seriate, 1–8 cells high	Most uniseriate, 1–16 cells high	Mainly uniseriate, 1–14 cells high	Probably all uniseriate, 1–9 cells high
Number of rays per mm ² in tangential section	—	35–50	30 (silicified specimen) 60 (fusain)	About 45–80 (fusain)
Resinous ray cell	Unknown	Present	Present	Probably present

section. The rays are somewhat higher (up to ten to sixteen cells) and there are more pits in the cross fields. I cannot confirm the presence in the Chinese wood of similar specialized, narrow resin cells as in the rays of *P. aveiroense*, though some of the ray cells, as mentioned above, might be resinous. Septate tracheids, however, are unknown in the Portuguese wood.

The wood of *Pseudofrenelopsis parceramosa* Fontaine (Alvin *et al.* 1981) from the Barremian of England has much in common with the wood described here. Both have distinct but uneven growth rings and occasional septate tracheids in the late wood. Their tracheids, rays, and cross fields are similar to each other. The differences lie only in the number and dimension of cells and pits. The tracheids of the English wood are larger, and there are more pits in the cross field and cells in the ray. A possible substantial difference is the absence of convincing resinous tracheids in the Chinese wood.

Alvin *et al.* (1981, p. 774) have summarized the occurrences and structures of the secondary woods of cheirolepidiacean conifers. Their work shows that all the secondary woods having such an affinity, known from several different geological ages in Euramerica, have many features in common. This also applies to the secondary xylem here described from the Cretaceous of China. It is noteworthy that the structures of the secondary xylem of different members of Cheirolepidiaceae underwent very little change from Rhaetian to Maastrichtian times, although their leafy shoots display a great diversity in external morphology.

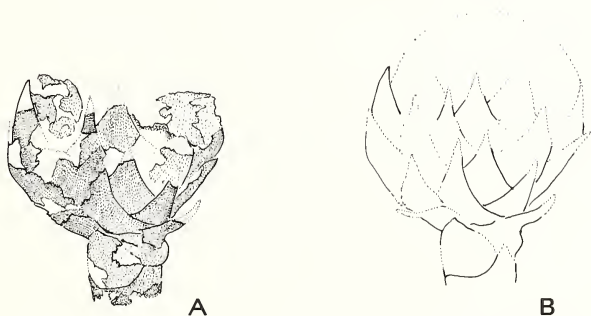
Associated male cone

Genus *Classostrobus* Alvin, Spicer and Watson 1978

Classostrobus cathayanus sp. nov.

Pl. 79, figs. 3–7; Pl. 80, figs. 1–7; text-fig. 4A, B

Diagnosis. Male cone borne on a short pedicel of 8 mm wide and 8 mm long (not complete), covered with broad leaves. Cone probably spherical, more than 20 mm long (apex not preserved) and 23 mm wide in the middle part. Microsporophylls borne spirally, with probably 2 + 3 parastichies, consisting of a slender stalk and a rhomboidal sporophyll head 7–10 mm high, 7–8 mm wide (exposed part 6–7 mm long and 4–5 mm wide). Apex acuminate. Abaxial cuticle of sporophyll head thick, consisting of polygonal cells, $40\text{--}60 \times 15\text{--}25 \mu\text{m}$ in size; anticlinal walls $3\text{--}10 \mu\text{m}$ thick; periclinal walls with a large conical papilla usually $15\text{--}37 \mu\text{m}$ long, but longer near margin. Cutinized hypodermis present, consisting of elongated cells, 25 to $> 100 \mu\text{m}$ long and $7\text{--}20 \mu\text{m}$ wide. Stomata not seen. Adaxial cuticle thinner, composed of elongated cells $40\text{--}90 \times 8\text{--}30 \mu\text{m}$, anticlinal walls thin ($1\text{--}8 \mu\text{m}$)



TEXT-FIG. 4. *Classostrobus cathayanus* sp. nov. (all are $\times 2$). A, holotype PB 10237, the same as Pl. 81, fig. 1; coaly substance shown by stippling; B, the same, stippling being omitted in order to show the shape of sporophylls clearly.

and straight; periclinal wall smooth. Stalk of sporophyll with very delicate cuticles, consisting of elongated cells about $10\text{ }\mu\text{m}$ wide. Pollen sacs situated in the basal part of the sporophyll. Membrane thin and delicate, with isodiametric cells, $10\text{--}24\text{ }\mu\text{m}$ in diameter.

Pollen of *Classopollis*-type, spheroidal with flattened poles, $26\text{--}41\text{ }\mu\text{m}$ in diameter (mean = 33.28 , s.d. = 3.57 ; thirty-five grains measured) in polar view, with a subequatorial circular furrow (rimula) situated at the distal edge of an equatorial band of about $7\text{--}8\text{ }\mu\text{m}$ in width; striations faintly developed, $5\text{--}7$ rows in the band. Distal pore (cryptopore) round, $6\text{--}9\text{ }\mu\text{m}$ in diameter. Proximal tetrad mark distinct; laesurae $2\text{--}8\text{ }\mu\text{m}$ long. Exine $1.0\text{--}1.5\text{ }\mu\text{m}$ thick with grumous-verrucose or occasionally echinulate external sculpture; inner surface smooth or nearly so.

Name. *Cathay*, a poetical name for China.

Remarks. Like many fossil male cones, *Classostrobus cathayanus* is incompletely known, but its generic determination seems to be certain as characteristic *Classopollis* pollen grains have been found *in situ*. Only two specimens have so far been found, both being incomplete and partly pyritized. The type specimen (Pl. 80, fig. 1) seems to have lost its apical portion. The arrangement of sporophylls suggests, however, that most parts of the cone are undistorted. Almost all the information about this species was obtained from this specimen. The other (not figured) was sacrificed for transfer preparation, but little information has been added. Neither intact pollen sacs nor pollen masses were found. The pollen sacs seem to have shed their pollen and only a few preparations from the lower part of the sporophylls yield fragments of pollen sac membrane with some adhering pollen grains. It is not possible to determine the number and exact position of the pollen sacs on the sporophyll.

No well-preserved specimen of sporophyll with a complete stalk still attached has been found in the debris. A fragment of sporophyll with a short stalk of about 1 mm long, still attached, was obtained. The attachment of pollen sacs on the sporophyll, however, is not shown on this specimen. The cuticle of the stalk is very thin. Usually, it dissolves in ammonia. Only one preparation shows the outline of the elongate cells (not figured).

The abaxial surface of the sporophyll is covered with papillate thickening. Outlines of epidermal cells can only be seen on the inner side of the cuticle. No convincing stomata were found in spite of prolonged searching. The abaxial cuticle of a leaf on the pedicel has almost the same structure (Pl. 79, fig. 5).

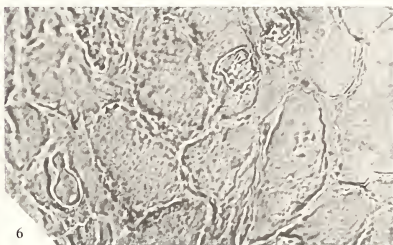
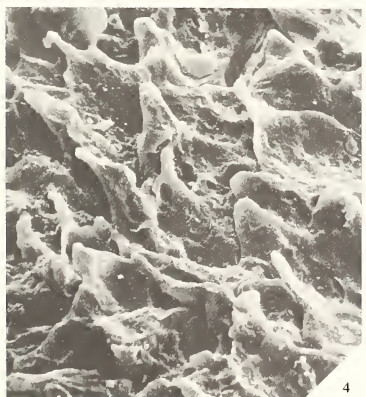
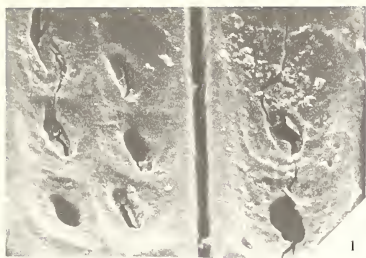
The exine of pollen consists of only one layer, nothing like a nexine being seen in the slides.

Comparison. *C. cathayanus* which, if interpreted correctly, attains a size of more than 20 mm long and 23 mm wide, is the largest male cone so far known to me amongst Cheilepidiaceae conifers. It also has the largest sporophylls which are distinguished from those of most male cones known of this extinct family by having a long and acuminate apex, instead of a short and broadly acute one (Archangel'sky 1968; Barnard 1968; Muir and van Konijnenburg-van Cittert 1970; Hlušík and Konzalová 1976; Chow and Tsao 1977; Pons 1979). The cuticular structures of sporophylls, however, are essentially similar to each other in having a thick epidermal cuticle with well-developed cutinized

EXPLANATION OF PLATE 79

Figs. 1–2. Secondary xylem; all are SEM photographs and from PB 10242. 1, two cross fields showing two and six bordered pits respectively, $\times 3000$. 2, radial fracture showing the ray cells and pits in the cross fields, tracheids of the late wood on the left of the figure, $\times 400$.

Figs. 3–7. *Classostrobus cathayanus* sp. nov.; all are from PB 10237; 3 and 6 are light micrographs. 3, abaxial cuticle of a sporophyll showing elongated hypodermal cells and polygonal epidermal cells with conical papillae, $\times 500$. 4, outer surface of the abaxial cuticle of a sporophyll, showing conical papillae, $\times 700$. 5, inner surface of the abaxial cuticle of a leaf on the pedicel, showing polygonal epidermal cells and elongated hypodermal cells, $\times 500$. 6, adaxial cuticle of a sporophyll showing more or less elongated cells, $\times 500$. 7, fragment of the membrane of a pollen sac with isodiametric cells and one adhering pollen grain, $\times 700$.



hypodermis and a thinner adaxial cuticle. The abaxial cuticles of *C. cathayanus* recall especially those of *C. comptonensis* (Alvin *et al.* 1978), in having conical papillae on the periclinal walls, though no stomata were seen. The adaxial cuticles of the two species are different. No papillae have been seen on the periclinal wall of those of the present species.

There is a general similarity in appearance between the pollen grains of *C. cathayanus* and those of the other members of the Cheirolepidiaceae. In respect of their size and their feeble equatorial striations, the pollen grains resemble those of *Brachyphyllum crucis* Kendall (van Konijnenburg-van Cittert 1971, 1972; Harris 1979), *B. scotti* (Kendall 1949), and *Frenelopsis oligostomata* Romariz (Pons and Brouton 1978), but the external sculpture is somewhat different. Internal sculpture of the pollen of *C. cathayanus* is scarcely visible, if present at all. The pollen grains described here might also be compared with some dispersed *Classopollis* species with weakly developed internal sculptures and striations, such as *C. simplex* and *C. keiseri* (Reyre 1970), but they are distinguished by their size and external sculptures.

Attribution. Though a direct connection has not been proved, I am convinced that *C. cathayanus* belongs to *Suturovagina intermedia*, because the latter is the only conifer which could be a *Classopollis*-producer that has so far been found in the material. As no stomata have been seen on the cuticles of the sporophyll and the leaf on the pedicel, an identity in cuticular structure between the cone and the leafy shoot cannot be established. The hairy epidermal cells of the sporophyll differ also very much from those of *S. intermedia* in appearance. Such differences, however, might be expected between a sporophyll and an ordinary leaf of a conifer. As is known, Cheirolepidiaceae male cones sometimes do have very sparse or even no stomata on the abaxial cuticle of the sporophylls (Alvin *et al.* 1978; Harris 1957). The hairy epidermis is a rather common phenomenon of cone scale of conifers, especially the female cone scale, e.g. *Cedrus deodara*.

GENERAL DISCUSSION

A revised study of *S. intermedia* based on the newly collected abundant material has revealed the following main points:

1. The shoots vary considerably in the shapes of their leaves. The mature shoot bears mainly broad leaves encircling the large part or the whole of the stem with either a gap or a suture between the two lateral edges. The shoot believed to represent the juvenile one bears scale leaves at intervals. Abnormal shoots with continuing spiral leaves have also been noted.

2. The cuticular structures of the leaf display no great variation in different shoots. The characteristic stomata differ from those of all other genera so far known in Cheirolepidiaceae.

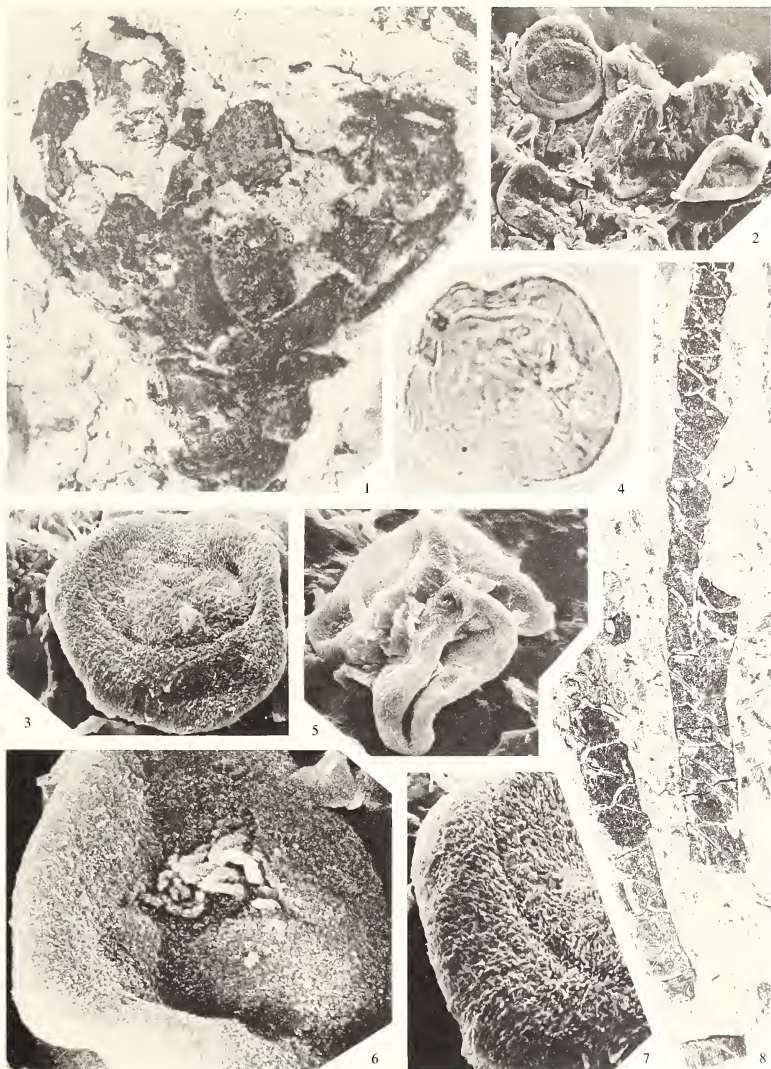
3. The dispersed fossil secondary xylem shares all the common features of some other members of this family. The attribution of it to *S. intermedia* is based on the close association and the similarity in tracheids between the dispersed and *in situ* secondary xylem.

4. The associated male cone referred to *S. intermedia* yields *Classopollis* pollen, though continuity has not been demonstrated.

EXPLANATION OF PLATE 80

Figs. 1-7. *Classostrobus cathayanus* sp. nov.; all are from PB 10237; 2, 3, 5-7 are SEM photographs. 1, holotype, $\times 4$ (in paraffin). 2, group of pollen grains, $\times 700$. 3, distal view of a pollen grain, showing the subequatorial circular furrow and the round pore, $\times c. 2000$. 4, a pollen grain showing faintly developed striations, $\times c. 1500$. 5, a tetrad, $\times 1300$. 6, part of a pollen grain in proximal view, showing strand-like elements in the triradial slit, $\times 2000$. 7, part of a pollen grain showing rimula and the surface sculpture, $\times 5000$.

Fig. 8. *Suturovagina intermedia* Chow and Tsao; branched hand specimen, $\times 1$ (in paraffin). PB 10238.



ZHOU, cheirolepidiaceus conifer

If, as I believe, all the above interpretations are correct, *S. intermedia* is a rather completely known Cheirolepidiaceae conifer which shows great variation in external morphology of leafy shoots. It is of interest that some types of these leafy shoots are unknown to me in any other conifers both living or fossil, although the secondary xylem and *Classopollis*-producing male cone are conventional in Cheirolepidiaceae. Alvin *et al.* (1978, p. 854) believe that the external morphological diversity of leafy shoot of different genera might well imply ecological diversity. The great morphological variation as well as overlap in characters between different genera suggests that during Jurassic and Cretaceous times Cheirolepidiaceae was a developing rather than a declining family.

Since fusain (fossil charcoal), as now accepted by many palaeobotanists, is a common product of natural wild fire (heath or forest fire) (Harris 1957, 1958; Batten 1974; Scott and Collinson 1978; Cope and Chaloner 1980; Alvin *et al.* 1981), its occurrence in the material indicates that the conditions in the Cretaceous of that part of China were sometimes favourable to the occurrence of wild fires. The distinct growth rings of secondary xylem suggest periodic droughts in which lightning was likely to occur.

So far, little is known about the shape and size of the whole *S. intermedia* plant. No well-preserved female cones were found in our material. The organization of the male cone still remains unclear and there is no direct evidence of the connection of the male cone to the leafy shoot. These gaps in information are expected to be filled in by further collection and study.

Cheirolepidiaceae conifers, so far as the present knowledge goes, are widely distributed in East China. From most localities, however, only a few specimens were collected, and these have not been carefully studied. It is to be hoped that these deficiencies will be made good by future work. The investigation of Cheirolepidiaceae conifers in this part of the world would certainly be helpful in forming a complete picture of the distribution, ecology, and evolution of this important, extinct family of Mesozoic conifers.

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SPIRALLY COILED 'COPROLITES' FROM THE UPPER TRIASSIC MALERI FORMATION, INDIA

by SOHAN L. JAIN

ABSTRACT. A new collection of coprolites exhibiting spiral markings from the upper Triassic Maleri Formation in the Pranhita-Godavari valley of southern India is critically examined. An attempt is made to relate their internal structure to the Maleri faunal elements. *Ceratodus* is a conspicuous member of the Maleri fauna. Some anatomical features such as the morphology of the spiral valve and faeces and the relationship between dental plates and body size in living *Neoceratodus forsteri* have been examined. The internal structure of the coprolites reveals the presence of a *scroll* valve which is quite dissimilar to the *spiral* valve of *Neoceratodus*. Critical assessment of the coprolites, based on external morphology and thin sections, does not support their determination as 'fossilized excrement', 'fossilized intestinal contents', or 'enterospirae' of *Ceratodus*. The evidence to relate the coprolites to other faunal members is equivocal. It is suggested that the 'coprolites' may belong to an as yet undetermined member of Maleri fauna.

THE study of coprolites has provided valuable information about certain aspects of the biology of the animals which have been associated with them (e.g. Zangerl and Richardson 1963; Williams 1972; Stewart 1978; Broughton *et al.* 1978; Sohn and Chatterjee 1979; Zidek 1980). The coprolites may indicate the nature of the large intestine, the food habits of the animal, and, indirectly, the environment in which it lived. There have been a number of interpretations of the precise nature of coprolites. They have been interpreted as 'fossilized vertebrate excrements', 'fossilized intestinal contents', or 'fossilized intestine or enterospirae' (see Williams 1972, for full references), produced, for example, by larger fishes preying upon smaller individuals of their own species (Zidak 1980) or by an otherwise unknown member of a fauna (Ash 1978). Some coprolites have also been identified as egg cases of elasmobranch fishes (Crookall 1930), land snails (Fritsch 1907), or even insect larvae (Langford 1963).

Coprolites from the upper Triassic Maleri Formation have been known since the nineteenth century (Oldham 1859) and a preliminary description was published eighty years later (Matley 1939a). A collection of 'rounded, oval or ellipsoidal' coprolites from the Maleri Formation has recently been examined by Sohn and Chatterjee (1979). They reached conclusions about the palaeoposition of India mainly on the basis of contained diagnostic freshwater ostracods. The present study is restricted to the cylindrical and spirally coiled coprolites and concerned largely with their biological nature; as such it may be regarded as complementary to that of Sohn and Chatterjee.

Three main aspects relating to the coprolites are considered: (1) their precise morphology, including that revealed in thin section; (2) the biological characteristics of the Maleri fauna, especially in relation to mode of life, food habits, and structural peculiarities of feeding and digestive apparatuses; and (3) the structure of the intestine (including spiral valve), faeces, and the ratio of dental plates to body size in *N. forsteri*, the extant Australian lungfish (chosen for comparison because *Ceratodus* is a conspicuous member of the Maleri fauna). Information on coprolites and associated faunas elsewhere was also considered. There is equivocal evidence to associate the coprolites with members of the Maleri fauna but they may not be their preserved faeces, gut contents, or enterospirae (see Zangerl and Richardson 1963).

MESOZOIC COPROLITE OCCURRENCES IN INDIA

Although coprolite occurrences have been sporadically mentioned along with fossil remains from various parts of the Indian peninsula, most are known from the Wardha and Pranhita-Godavari valleys. The following summary (and text-fig. 1) indicates the nature and occurrence of the material:

Wardha valley. Upper Cretaceous sediments near Pisdura; 600 specimens collected from which 350 were examined (Matley 1939*b*); ovoid, ribbed and subcylindrical in shape; associated with sauropod dinosaurs (titanosaurs) and chelonians.

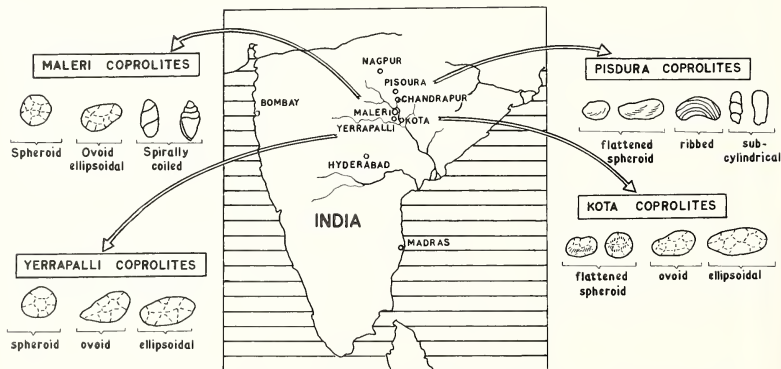
Pranhita-Godavari valley. 1. Lower Jurassic Kota Formation near Pochampalli (Jain *et al.* 1975); numerous specimens (not yet described); rounded, oval, or ellipsoidal with desiccation marks; associated with sauropod dinosaurs.

2. Upper Triassic Maleri Formation near Maleri; numerous specimens; spheroid, ovoid, ellipsoidal (with desiccation marks), and spirally coiled; associated with fish, amphibian, and reptile remains (Oldham 1859; King 1881; Matley 1939*a*; Sohn and Chatterjee 1979).

3. Late lower or early middle Triassic Yerrapalli Formation, near Yerrapalli; few specimens; spheroid or ovoid, with desiccation marks; different in shape and size from Maleri coprolites (Chatterjee 1967); associated with labyrinthodont (capitosaur), dicynodonts, erythrosuchid, and therapsids (Jain *et al.* 1964).

Terminology

The coprolites at Maleri vary in shape and size. They can be grouped broadly as non-spiral and spiral. The non-spiral coprolites may be rounded, ovoid, or ellipsoidal and are comparable to coprolites from other localities in India. The spirally coiled coprolites are, however, restricted in their distribution. Two types of spiral coprolites were recognized by Neumayer (1904) in the Permian of Texas. These categories were adopted by Williams (1972) in an exhaustive work on the origin of spiral coprolites. Spiral coprolites may be *heteropolar* (type A) 'characterised by a relatively large but variable number of closely spaced spiral turns concentrated on one end of the coprolite', or *amphipolar* (type B) 'characterised by a relatively small number of widely spaced spiral turns extending the length of specimen'. This terminology is adopted here since most of the coprolites under study fit the above definitions. However, a few coprolites which do not show clear spiral markings have been included because spiral features are seen in damaged portions of them. It is likely that coprolites with a flattened cylindrical shape are related in some manner to either type A or B. This third category termed here as *cylindrical* includes oblong-cylindrical, flattened cylindrical, and spindle-shaped coprolites.



TEXT-FIG. 1. Main localities and gross morphological features of Mesozoic coprolites in central India.

Material

All coprolite specimens used in the present study have been obtained from a locality close to Maleri (see Roychowdhury 1965, for locality map). A few poorly preserved specimens were also collected from a site near Angrezpalli, close to Maleri. *Ceratodus* teeth are common in both localities.

The nature of the occurrence of coprolites in the Maleri was noted by King (1881, pp. 121-122): 'The commonest remains are coprolites which lie about the field in large numbers, of all sizes and shapes, from the short cylindrical form with tapering ends and spiral foldings up to large flat rudely discoidal coils.' Subsequently, Aiyengar (1937, p. 104) remarked that 'Coprolites are abundant about a mile W.S.W. of Maleri. They are generally greenish yellow in colour varying in size from that of a walnut to a coconut. In shape some are flat and cake like, some cylindrical, spiral, reniform or botryoidal. In cross-section they present a central core surrounded by layers of iron-impregnated material.' Matley (1939a) made a detailed study of sixteen specimens collected by Hughes in 1876, plus one added at a later date.

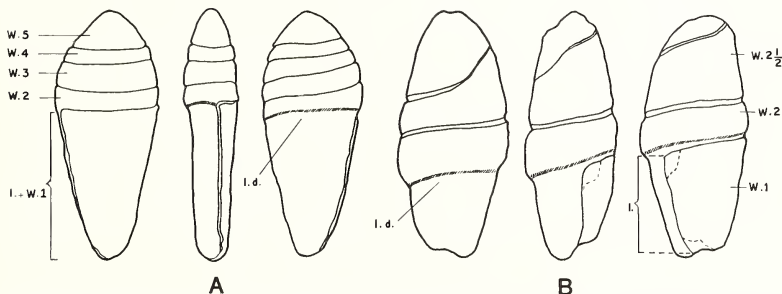
Sohn and Chatterjee (1979) have recently studied a collection of twelve coprolites from a site near Achalapur (within the Maleri Formation), a few kilometres from Maleri. The coprolites are fairly large, heavy, rounded, oval, or ellipsoidal, averaging 70×50 to 100×80 mm. This site has not yet yielded spirally coiled coprolites but is otherwise well known for Maleri vertebrates. All the specimens of the labyrinthodont amphibian *Metoposaurus maleriensis* described by Roychowdhury (1965, p. 12), were obtained from a locality north-west of Achalapur. Subholostean fish were also found near Achalapur in 1958 (Jain *et al.* 1964; Jain 1980).

The registration number of all specimens mentioned in the text, including thin sections, refer to the Palaeontological Collections, Indian Statistical Institute (I.S.I.), Calcutta.

DESCRIPTION OF THE COPROLITES

Gross morphology. The collection includes forty-three specimens; twenty-five collected prior to 1978 and the remaining eighteen during the 1979-80 field season. Of these twenty-one are amphipolar, nine heteropolar, and the remaining oblong-cylindrical, flattened-cylindrical, or spindle shaped. A number of specimens of cylindrical coprolites are illustrated in Pl. 81, figs. 1-7, 10. Some are cylindrical with rounded ends (Pl. 81, figs. 2, 3), one resembles a flattened pebble (Pl. 81, fig. 10), and some show faint spiral markings (Pl. 81, figs. 4-7). Embedded ganoid fish scales have been observed in some coprolites (Pl. 81, fig. 3). The length of these coprolites varies between 27 and 40 mm with a maximum diameter of 10 to 32 mm, and minimum diameter 0.9 to 27 mm.

The *amphipolar* type of coprolite (text-fig. 2B) is robust in appearance and oval to circular in cross-section. The lip extends to less than half the length. The number of complete coils in the whorl varies between two and four and a half and a distinct lip depression (l.d.) is present. In P. 56 (Pl. 81, figs. 8-9) the whorl is displaced in the middle. The coil has a thickness of 32 mm. P. 78 is the largest coprolite in the collection measuring $79 \times 30 \times 27$ mm. It exhibits the usual features of such coprolites, except displacement of the lip. Two other



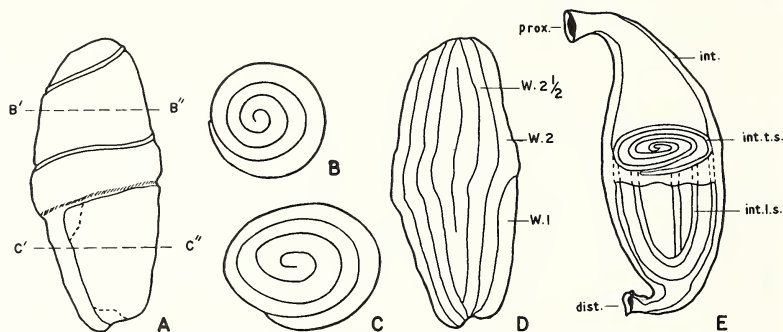
TEXT-FIG. 2. Gross morphology of spiral coprolites from the Maleri Formation, India. A, heteropolar coprolite (based on ISI P. 49), and B, amphipolar coprolite (based on ISI P. 51) in obverse, lateral, and reverse views. l., lip of the whorl; l.d., lip depression; w. 1-w. 5, whorls, 1-5 of the coil.

coprolites, P. 82 and P. 90, are embedded in oval sheaths (cf. Matley 1939a, fig. 7) but are partly exposed to exhibit amphipolar features. The dimensions of these coprolites range as follows: total length 34–79 mm, maximum diameter 18–40 mm, minimum diameter 13–30 mm, and maximum width of the lip 20–23 mm.

The *heteropolar* type of coprolite (text-fig. 2A) is shaped like a snail shell. The whorl starts with a wide 'lip' extending to more than half of the total length of the specimen and is then thrown into several narrow coils ending in a smooth conical termination. Most specimens exhibit lateral compaction. P. 80 is the smallest heteropolar coprolite ($45 \times 17 \times 14$ mm) and P. 91 the largest ($66 \times 28 \times 22$ mm) but it is highly encrusted, which obviously exaggerates the dimensions. The heteropolar coprolites exhibit two and a half to five complete whorls which are sometimes obscured by abrasion. There is a distinct lip depression (l.d.) which is evident on the surface opposite to the lip area. The dimensions of these coprolites range as follows: total length 45–66 mm, maximum diameter 17–28 mm, minimum diameter 14–26 mm, and maximum width of the lip 26–42 mm. The thickness of the lip varies from 2.5 to 3.5 mm at the lip region.

Thin section studies. A cylindrical coprolite (P. 57) abraded and damaged at one end, was polished and found to have three whorls in cross-section, each approximately 1.7 mm thick.

One amphipolar coprolite (P. 75) was prepared as a polished transverse section. This revealed three complete and close-set whorls varying from 1.4 to 1.6 mm in thickness. A series of longitudinal sections of another



TEXT-FIG. 3. The anatomical interpretation of an amphipolar coprolite from the Maleri Formation, India. A, gross morphology. B and C, transverse sections (semi-diagrammatic, based on present studies and Matley 1939a) in the region B'-B'' and C'-C'' of A. D, longitudinal section (simplified from Matley 1939a). E, reconstruction of intestine with scroll valve in transverse and longitudinal section. int., intestine; int. t.s., intestine in transverse section; int. l.s., intestine in longitudinal section; prox., proximal end; dist., distal end; w. 1-w. 2½, whorls of the coil.

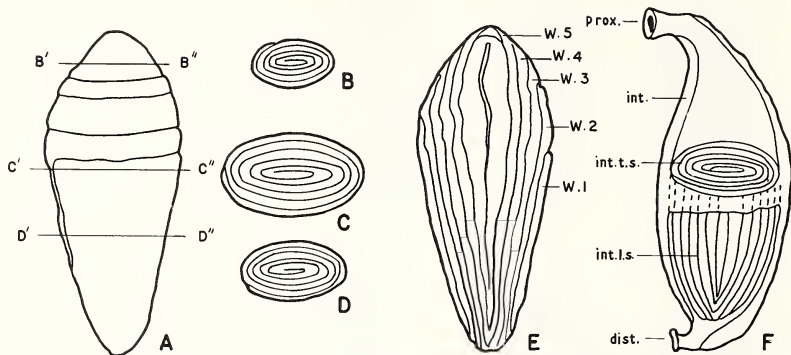
EXPLANATION OF PLATE 81

Figs. 1–18. Cylindrical and amphipolar coprolites from Maleri Formation, India. 1–3, cylindrical coprolites: 1, ISI P. 52, $\times 1.2$; 2, ISI P. 53, $\times 1.5$; 3, ISI P. 54, ganoid scales indicated by arrow, $\times 1.1$. 4, 5, oblong coprolite with spiral markings: 4, obverse; 5, reverse, ISI P. 50, $\times 0.9$. 6, 7, oval-elongated coprolite with spiral marking: 6, obverse; 7, reverse, ISI P. 61, $\times 1.1$. 8, 9, amphipolar coprolite with displaced coil in the middle: 8, obverse; 9, reverse, ISI P. 56, $\times 0.8$. 10, cylindrical-flattened coprolite with faint spiral markings, ISI P. 71, $\times 1$. 11, 12, amphipolar coprolite (also shown in text-fig. 2A and 3A) with well-marked coils and lip: 11, obverse; 12, reverse, ISI P. 49, $\times 0.9$. 13, 14, amphipolar coprolite, damaged at both ends: 13, obverse; 14, reverse ISI P. 68, $\times 0.64$. 15, 16, amphipolar coprolite, somewhat damaged: 15, obverse; 16, reverse, ISI P. 69, $\times 0.9$. 17, 18, amphipolar coprolite from Matley (1939), GSI collection: 17, longitudinal section, $\times 2$; 18, transverse section, $\times 1$.



amphipolar coprolite (P. 77) revealed the presence of calcium phosphate granules and fish scales in between parallel folds. Longitudinal and transverse sections of amphipolar coprolites, reproduced here (Pl. 81, figs. 17-18) from Matley (1939a), bear a close resemblance to the specimens studied here. These reveal the presence of two and a half to three whorls of scroll and show that the faecal mater was compacted. The scroll valve in the intestine as evidenced by amphipolar coprolites from Maleri is reconstructed in text-fig. 3.

One heteropolar coprolite (P. 70) was sectioned longitudinally (Pl. 82, figs. 7, 8). The whorls run along the whole length of the coprolite and do not exhibit any valves or spirals in between. The specimen is seen to have a coil of five whorls before sectioning (Pl. 82, figs. 3 and 4). The outer two have been peeled off and the remaining three are visible in the section. The thickness of the whorls varies from the outer which are approximately 2 mm to the inner which are 1.0 to 1.5 mm thick. Another heteropolar coprolite (P. 76) was cut into a series of eight transverse sections. These have revealed the presence of a single coil in the intestine thrown into five whorls. The whorls are compact and close set and are filled with mineral, mostly calcium phosphate. The scroll valve as evidenced by heteropolar coprolites is reconstructed in text-fig. 4.



TEXT-FIG. 4. The anatomical interpretation of a heteropolar coprolite from the Maleri Formation, India. A, gross morphology. B, C, and D, transverse sections (semi-diagrammatic, based on thin section studies) in the region B'-B'', C'-C'', and D'-D'' of A. E, longitudinal section (restored and simplified). F, reconstruction of intestine with scroll valve in transverse and longitudinal section. dist., distal end; int., intestine; int. t.s., intestine in transverse section; int. l.s., intestine in longitudinal section; prox., proximal end; w. 1-w. 5, whorls of the coil.

EXPLANATION OF PLATE 82

Heteropolar coprolites from Maleri Formation, India.

Figs. 1-6. Some selected heteropolar coprolites. 1, 2, obverse and reverse of ISI P. 59, $\times 0.7$. 3, 4, obverse and reverse of ISI P. 70, $\times 0.8$. 5, 6, obverse and reverse of ISI P. 58, $\times 0.7$.

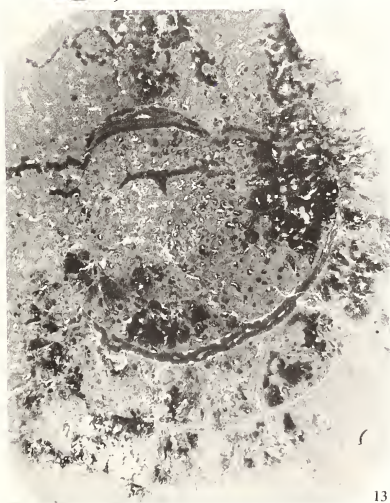
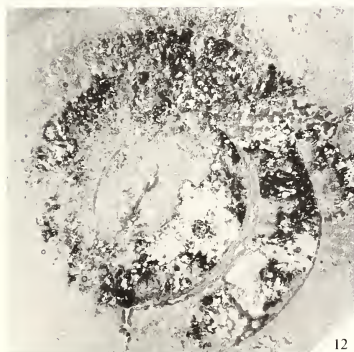
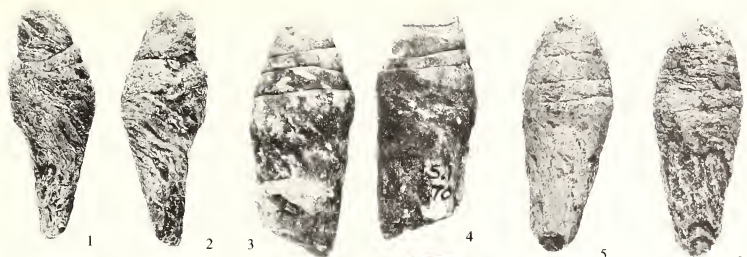
Figs. 7, 8. Longitudinal section (bisected halves) of ISI P. 70, $\times 1.6$; the sections represent only the inner core as two layers have been peeled off during section cutting (see text for details).

Fig. 9. A heteropolar coprolite from Matley (1939a) GSI collection, K. 42/419, $\times 1.2$, showing five spirals.

Fig. 10, 11. Obverse (10) and reverse (11) of an undamaged coprolite, ISI P. 51, $\times 0.8$; also shown in text-figs. 2b and 4a.

Figs. 12, 13. Transverse sections of ISI P. 76, showing the disposition of whorls of the coil and mucosal folds.

12, showing compact contents of lumen of the intestine with mucosal folds (serial section no. 3), $\times 4.3$.
13, showing mucosal folds, restricted to the lining of the inner whorls of the coil (serial section no. 7), $\times 5.5$.



In some thin sections of P. 76, features which may be interpreted as impressions of mucosal folds have been preserved (Pl. 82, figs. 12, 13). These thin sections show features somewhat similar to the transverse section of a fish intestine (illustrated by Williams 1972, pl. 3, figs. 3, 4). However, there are three main differences. First, the impressions of mucosal folds in the Maleri coprolites are seen only in a few thin sections and in very limited areas, generally in the inner coils of the whorl. Secondly, the mucosal folds are double in the inner coils but single in the outer ones (Pl. 82, fig. 12; Pl. 83, figs. 1, 2) and occupy only a fraction of the total thickness of the coil. Thirdly, the mucosal folds are very gently thrown into shallow corrugations (Pl. 83, figs. 3, 4) and do not seem to have complex folded features as indicated by Williams (1972, pls. 4-7). These corrugations may be continuous or discontinuous. Thin section studies by Williams show that the thickness of each coil of the whorl is almost wholly occupied by arborescent mucosal folds. The Maleri coprolite thin sections, on the other hand, suggest that the thickness is largely contributed by intestinal inclusions which have been replaced by different minerals (mostly calcium phosphate). It is interesting to make a comparison of a transverse section of a spiral valve of a dogfish (Williams 1972, pl. 2, figs. 1, 2) and a heteropolar 'spiral coprolite' from the lower Permian. It reveals that there is a considerable space for food materials in the lumen of the gut between two adjacent folds in the dogfish intestine. On the other hand, Williams has identified complex folds in the same area in the heteropolar coprolite. His photographs are undoubtedly most convincing. However, it may be argued that the folds represent sculpturing produced by the passage of faecal materials over mucosal folds.

Remarks. Two important conclusions may be drawn from this study: (1) although heteropolar, amphipolar, and some cylindrical Maleri coprolites have different external morphologies their internal features are more or less alike, differing only in the number of whorls; and (2) the coprolites suggest a scroll valve type of intestine in which one flap of the coil is attached to the intestinal wall and the remaining whorl is rolled up like a scroll of paper.

These results are at variance with the conclusions of Williams (1972, p. 13) who has suggested that heteropolar coprolites have a 'configuration (which) is fully consistent with the morphology of the spiral valve . . .'. It may be mentioned that it is not always possible to interpret the internal features as being related to a scroll or spiral valve exclusively on the basis of transverse sections. The longitudinal sections, on the other hand, reveal the true nature of the valve. Williams and other recent workers have largely illustrated their work with transverse sections. It is likely that longitudinal sections of the specimens may reveal their true nature.

THE MALERI FAUNA

A review of the Maleri fauna is attempted below to designate or narrow down the possible candidates for possession of an intestine with a scroll valve. The fauna is well known (Chatterjee 1978; Sohn and Chatterjee 1979; Jain 1980). Fishes, amphibians, and reptiles are well represented and bivalves and ostracods are known to occur.

Fishes. A few species of a lungfish, *Ceratodus* (Miall 1878; Jain 1968; Shah and Satsangi 1969; Chatterjee and Roychowdhury 1974) and one species of a freshwater elasmobranch, *Xenacanthus* (Jain 1980) are known from the Maleri formation. In addition, there is evidence of a small subholostean fish (Jain *et al.* 1964). *Ceratodus* is comparable to the extant *N. forsteri* of Queensland (described in detail below), in having comb-like ridged mandibular and palatal dental plates in addition to a pair of small vomerine teeth. The Maleri *Ceratodus* may range from 1 to 2 m in length.

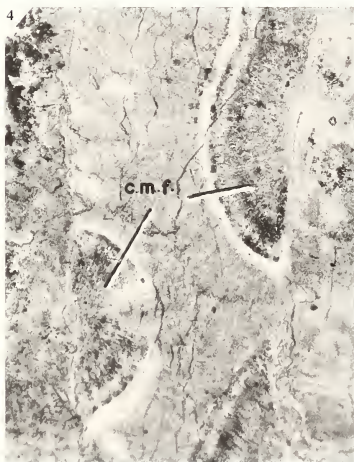
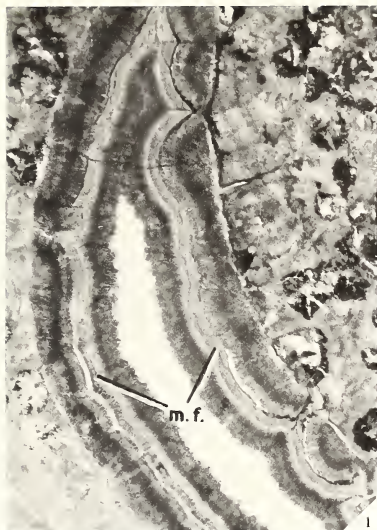
EXPLANATION OF PLATE 83

Thin sections of Maleri Coprolites.

Fig. 1. A portion of thin section (TS serial no. 4) of ISI P. 76 to show mucosal fold (m.f.) and the lumen, $\times 105$.

Fig. 2. A portion of thin section (TS serial no. 3) of ISI P. 76 to show closely spaced double mucosal folds (d.m.f.) (enlargement from Pl. 82, fig. 12), $\times 105$.

Figs. 3, 4. Photomicrographs of a portion of thin section (TS serial no. 5) of ISI P. 76 to show corrugated mucosal folds (c.m.f.) as 3, continuous and 4, discontinuous bands, $\times 105$.



The Xenacanth is estimated to be about 1.2 m long, predaceous, and a swift swimmer. A spiral valve is present in the intestine of *X. decheni* (lower Permian of Bohemia, Czechoslovakia) which is one of the species in which the body is preserved. The subholostean was a 'small fish since the preserved head is no more than 25 mm' (Jain 1980). It probably fed by nibbling on aquatic vegetation, and fell an easy prey to piscivorous phytosaurs.

Amphibians. A metoposaurid amphibian, *Metoposaurus maleriensis*, has been described by Roychowdhury (1965). The large labyrinthodonts were probably sluggish creatures generally inhabiting bottom waters and feeding upon unwary prey. The teeth are indicative of carnivorous habit. Spiral coprolites have not been found associated with the Maleri metoposaurid.

Reptiles. The most common member is a rhynchosaur, *Paradapedon huxleyi* (Chatterjee 1974), which grows up to 1.4 m and was not adapted to an aquatic mode of life. It fed on vegetable foods such as rhizomes and seeds or mussels as available (Chatterjee 1980a). A phytosaur, *Parasuchus hislopi*, attaining a length of up to 2.7 m, is also known (Chatterjee 1978). The animal lived for the most part in water but made occasional excursions on land particularly during egg laying. Among other reptiles is an eosuchian, *Malerisaurus robinsonae* (Chatterjee 1980b), a cynodont, *Exaeretodon statisticae* (Chatterjee 1982), an aetosaur, similar to *Typothorax*, a thecodontosaur, and a coelurid. With the exception of the eosuchian, these were all land animals. Chatterjee (1980b, p. 187) argued that *M. robinsonae* may have found it advantageous to escape into tree branches from potential predators and its food may have consisted of insects and snails. The Maleri cynodont was a herbivore with specialized post-canine 'molariform' teeth (Chatterjee 1982, p. 203).

An attempt has been made recently (Jain 1980) to relate the more important members of the Maleri fauna to a possible food chain and ecology. Sohn and Chatterjee (1979) have already speculated about the producer of the rounded, oval, or ellipsoidal coprolites. They have suggested that (1) these are possibly droppings on the ground because a few specimens show surface cracks and (2) their large size suggests that they came from a large animal, e.g. a rhynchosaur. These large reptiles were abundant. They could have produced them as faecal excrement, but it is also possible that any other land animal from the Maleri fauna may have also produced them.

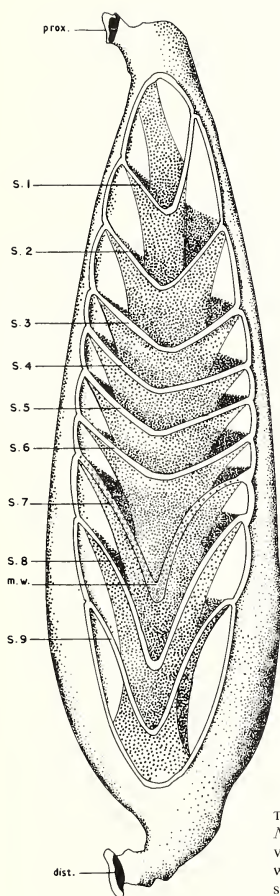
SPIRAL VALVE, FAECES, AND THE RELATIONSHIP OF DENTAL PLATE TO BODY LENGTH IN *NEOCERATODUS FORSTERI*

Spiral valve. The precise structure of the spiral valve of *N. forsteri* has not been figured in any current literature, though Jollie (1972) figures the gut of *Protopterus* showing the spiral valve and distinct stomach. Through the courtesy of Dr. Anne Warren, I obtained a specimen of the intestine of *N. forsteri* (text-fig. 5) removed from a fish 102 cm long.

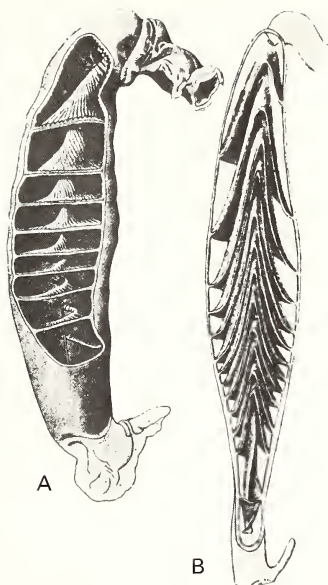
The spiral valve is present throughout the length of the sac-like intestine which is about 27 cm long and 9 cm at its maximum diameter in the lower one-third. The valve is of the shape of a carpenter's auger or a staircase with nine loose spirals of variable dimensions. The rectum opens into a small cloaca. The nine spirals increase in depth posteriorly. The seventh, eighth, and ninth folds are very deep and may be as much as three to four times larger than the anterior ones. The seventh fold is highly muscular (text-fig. 5).

The presence of a spiral valve in the intestine, as a device to increase the surface area for absorption, is known in many early vertebrates. It is present in cyclostomes and in all bony fishes except teleosts. A great deal of diversity is exhibited by the spiral valve of modern sharks. In *Raja* and *Scyllium* (text-fig. 6A, B) the spiral valve consists of a series of cones with their apices directed anteriorly but the configuration and depth of cones varies considerably between the two. A spiral valve is present in all the three-surviving dipnoans, though it is probably more primitive in *Neoceratodus* than in *Lepidosiren* and *Protopterus*. The folds of spiral in *Neoceratodus* are disposed as if a number of funnels of varying sizes were placed one on the top of another in series. In *Protopterus* the funnels face in the opposite direction in a fashion similar to a typical shark, *Callorhynchus* or *Acipenser*, as illustrated by Romer (1966). The disposition of intestinal folds in *Neoceratodus* is somewhat similar to those figured in Greenwood (1963) for a ray (*Raja* sp.). In a minority of sharks (e.g. *Scoliodon* sp.) the base of the valve twists but little and hence is relatively short; the valve fold, however, is highly developed and rolled up into a great scroll running the length of the intestine. This is referred to as a scroll valve, as distinct from spiral valve, but has the same function of increasing the area of absorption.

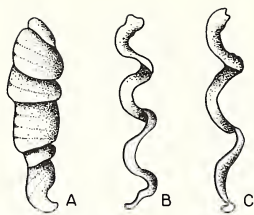
Faeces. Information on *N. forsteri* faecal matter has been provided by Dr. Anne Kemp who writes (pers. comm., 25 September 1979): 'In my experience the faeces of adult lungfish are loosely spiral but they usually fall apart. Juveniles produce much closer spirals.' Her photographs showing faecal pellets after ejection and following



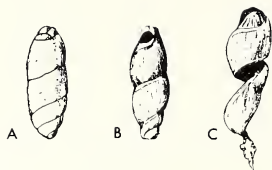
TEXT-FIG. 5. A dissected intestine (semi-diagrammatic) of *Neoceratodus forsteri*, showing morphology of the spiral valve ($\times \frac{1}{2}$). dist., distal end of intestine; m. w., muscular wall of the seventh valve; prox., proximal; s. 1 to s. 9, spiral valve whorls.



TEXT-FIG. 6. Valvular intestine of two sharks to show basic patterns. A, *Raja* (from Daniel 1934, after Paul Meyer); B, *Scyllium* (from Parker 1885).



TEXT-FIG. 7. Drawings of faecal material (actual size 3–5 cm) of *Neoceratodus forsteri*, based on photographs. A, at the time of deposition; B, after remaining in water for several hours, and C, after twenty-four hours.



TEXT-FIG. 8. Faecal material of modern lungfish *Protopterus annectans*. A, at the time of deposition B, after remaining in water for several hours, and C, after twenty-four hours (from Dean 1903).

several hours in water provided the basis for text-fig. 7. Dean (1903) figured spiral faecal pellets produced by the African lungfish *Protopterus annectans* (text-fig. 8). The faecal pellet is thrown initially into at least four compact spirals which become somewhat loosened after remaining in water for several hours. After twenty-four hours it becomes like a spiral ribbon. It may be noted that the faecal pellets of *N. forsteri* and *P. annectans* are closely similar in shape. In the former the pellet is less compact than in the latter. No information is available on the faeces of *Lepidosiren*, the South American lungfish. There is an almost virtual absence of information on the shape of modern shark faecal pellets. Williams (1972, p. 9) quotes from Dr. P. W. Gilbert who never found pellets of any type in shark pools, 'the material egested from the cloaca of a shark is either in a liquid or loosely viscous form'.

Dental plate-body size relation. No information seems to have been recorded on the relationship between the size of the dental plate and the body of *N. forsteri*. In view of the close resemblance of dental plates in the Triassic *Ceratodus* and *N. forsteri* this proportion could be utilized to estimate the size of extinct species. A single measurable specimen of *N. forsteri* 800 mm long in the collections of the Museum of Natural History, University of Kansas has a dental plate 30 mm long. Thus the dental plate/body length ratio is 3:80.

On the basis of range of teeth size the Maleri *Ceratodus* is estimated to have been 1–2 m long, but it is emphasized that dental plate size changes dramatically throughout growth.

DISCUSSION

A variety of vertebrates and invertebrates comprise the rich faunal assemblage in the Maleri. It is unlikely that any invertebrate could have produced the coprolites in question. Among the vertebrates the Maleri tetrapods are either aquatic, semi-aquatic, or land animals. In the foregoing account it has been suggested that none of them is likely to have had a spiral or scroll valve in the intestine. This is further supported by the general remark of Romer (1966, p. 356) who, while discussing spiralled features in the intestine, said that 'no living tetrapod has the slightest trace of this organ'.

There is no definite evidence of a scroll or a spiral valve in any fossil tetrapod. However, Charig (1979, p. 30) has illustrated an enormous coprolite (29 cm long) with a distinct whorl of seven spirals, as 'possibly' from a dinosaur. The locality and age are not given. The spirals have a maximum diameter in the middle of the specimen and the spiral structure is continued for the whole length. As such it can be called an amphipolar coprolite. In our own experience of collection of a large number of coprolites from a lower Jurassic locality in India, along with numerous sauropod dinosaur bones, we have never come across such spiral coprolites. All the coprolites are either rounded, oval, or ellipsoidal, usually with desiccation marks, similar to recent drying cow-dung. As such, Charig's specimen, though intriguing, must await confirmation of its association with the dinosaurs.

The records of coprolites with spiral markings reveals that they may occur at localities which have not yielded an animal with a spiral valve. Coprolites studied by Broughton *et al.* (1978) from the late Cretaceous Whitemud Formation of Western Canada exhibit coiling, folding, and contraction marks but are not spirally coiled and are quite distinct from the Maleri coprolites. The following examples, however, are worth noting:

1. Middle Triassic of Mendoza, Argentina (Rusconi 1949): spiral coprolites associated with *Typhothorax*, an actosaur.
2. Lower Lias of Lyme Regis, Britain (Buckland 1829; Pollard 1968): spiral coprolites associated with ichthyosaurs.
3. Upper Triassic rocks on the north-eastern shore of Lake Inder, U.S.S.R. (Ochev 1974): spiral coprolites associated with labyrinthodonts, dicynodonts, thecodonts, and theriodonts.

In addition amphibians, e.g. *Eryops* and *Diplocaulus*, have been considered the producers of heteropolar and amphipolar coprolites (Neumayer 1904).

In view of the fact that a spiral intestine has never been found in any living tetrapod it is unlikely that the tetrapods listed above produced the associated coprolites. It is, however, possible that new faunal elements, including fishes in which a spiral valve is widespread, will be discovered with the above occurrences in the future.

TABLE 1. The Maleri Fish

DIPNOI:		
<i>Ceratodus</i>	<i>C. hislopianus</i>	Described by Oldham (1859); commented on by Miall (1878); suggested size of the fish 1 to 2 m (Jain 1980).
	<i>C. hunterianus</i>	
	<i>C. virapa</i>	
	<i>C. nageswari</i>	Described by Shah and Satsangi (1969); smaller in size than above species.
ELASMOBRANCHII:		
<i>Xenacanthus</i>	<i>X. indicus</i>	Presence of <i>Xenacanth</i> suggested by Jain <i>et al.</i> (1964); described by Jain (1980); suggested size 1.2 m.
SUBHOLOSTEI:		
Unnamed genus and species		Presence mentioned by Jain <i>et al.</i> (1964); discussed by Jain (1980); size of head 25 mm, suggested size of fish 6-8 cm.

The possibility that the Maleri fishes (Table 1) produced the spiral coprolites raises three questions: 1. How widespread is the occurrence of a spiral valve in fishes? 2. Do fishes having a spiral (or scroll) valve pass faeces with spiral markings? 3. Are there any examples of fossil fish in which spiral structures have been found inside the body or close to it?

Romer (1966, pp. 355-356) provided an answer to question 1: 'This (spiral intestine) is characteristically developed in elasmobranchs in which it is typically a large cigar shaped body, extending nearly straight anteroposteriorly and occupying most of the length of the abdomen.' For the remaining fishes Romer has this to say: 'The spiral intestine is present in chimeras and to some degree in cyclostomes, and fossils even demonstrate its presence in the ancient class of Placoderms. Further, it was present in the early bony fishes, for living lungfishes and all lower actinopterygians retain a spiral valve, and even a few teleosts have a vestige of this structure.'

The available information on question 2 is somewhat contradictory. Although a spiral valve is known to be present in a number of extant shark species, faecal pellets of the same are unknown. Definite evidence of the presence of spiral features in the faecal material of extant fishes is available only in the dipnoans *P. annectens* (Dean 1903) and *N. forsteri* (present study), and in the holosteans *Amia* and *Lepisosteus* (Williams 1972). These fishes have a definite spiral valve in the intestine.

Regarding question 3, there are at least four good examples of inclusions with spiral markings within the preserved body of fish. Dean (1903) figured and described a specimen of *Cladoselache newberryi* in which a cast of the intestinal wall gives a direct evidence of the presence of a spiral valve. Zangerl and Richardson (1963) mentioned the presence of a spiral coprolite in the pelvic region of a mutilated shark specimen from the Pennsylvanian of Indiana. Zidek (1980) found a spiral coprolite in the tail region of *Acanthodes* from the Mississippian of Montana. Fritsch (1907) figured a shark, *Xenacanthus decheni* (lower Permian, Czechoslovakia), in which the spiral valve of the intestine occurs in its natural position, and also found a number of isolated bodies, having similar features, besides the skeleton of the same fish.

The spiral coprolites do not exhibit desiccation marks, in contrast to the rounded, oval, or ellipsoidal forms, suggesting that they have been deposited in an aquatic environment. As noted by Duffin (1979, p. 199): 'It is unlikely that the spiral structure would be retained by the contents of the intestine after squeezing through the sphincter at the base of the small intestine and extrusion into the rectum.' The faeces of *Neoceratodus* and *Protopterus* are extruded in the form of spiralled ribbons which tend to change into loose spirals after exposure. It is difficult to visualize the preservation and fossilization of such bodies into compact coprolites.

A second possibility is that these coprolites are actually 'enterospirae' (see Fritsch 1907, Williams 1972). Williams has recognized detailed anatomical features of the intestinal wall in thin sections of spiral coprolites from the Permian and Cretaceous of Kansas. By contrast, spiral coprolites from the Rhaetic bone-beds never show evidence of the preservation of mucosal folds on the whorl interfaces in thin section (Duffin 1979). Similarly the anatomical features illustrated by Williams have not been observed in Maleri coprolites, though the presence of mucosal folds has been observed in some thin sections. The mucosal folds either perished before fossilization or were never present. Thus the Maleri coprolites cannot be designated 'enterospirae' *sensu stricto*.

A third possibility (suggested by Stewart 1978, p. 13 for spiral coprolites from the upper Cretaceous Niobrara Formation) is that they represent 'fossilized intestinal contents'. In this connection it may be significant that in *Scyllium* the spiralled intestine is filled with finely divided gut contents (Williams 1972), resembling mud, which sticks so tightly between successive cones of the spiral that it is difficult to remove it with a stream of water. Any intestine so filled would stand an excellent chance of being fossilized. Since sections of the Maleri coprolites reveal finely compacted contents, extraneous elements like fish scales being rare, these could be interpreted as 'fossilized intestinal contents'. If the coprolites are fossilized intestinal contents, their possible association with the Maleri *Ceratodus* merits consideration. Several species are represented which were variable in body length as indicated by the size of the dental plates. Over 60% of the dental plates in the collections from Maleri (over 250 specimens) at I.S.I are around 40 mm long and they range from 15 to 60 mm. This suggests large fish, averaging over 1.0 m but reaching up to 1.6 m, based on the comparison with *N. forsteri*. The spiral coprolites in the present collection range from 50–65 mm, except one specimen which is about 80 mm long. Matley (1939a) recorded a size range of 50–55 mm. Only one specimen in his collection was 74 mm. Thus 50–65 mm may be considered the normal size range of Maleri coprolites. The spiral intestine of *N. forsteri* studied measured 27 cm, from a fish 102 cm long, indicating a ratio of 1:3.7. Dissection and measurement of a large number of fish would provide more accurate figures but this is not important for the present discussion. If the Maleri *Ceratodus* was similar to *N. forsteri* (their dental plates show close similarity), then they might show somewhat similar proportions between body length and the length of intestine or 'fossilized intestinal contents'. However, the Maleri coprolites have a size range which is far too small to fit the robust Maleri *Ceratodus*, even allowing for possible shrinkage of intestine. It may be argued that the entire length of the intestine may not be represented by the coprolites and that it may not have been complete at the time of fossilization. The compactness of the intestine, however, favours entire preservation. Moreover, collections made for nearly a century indicate a limited size range. The spiral valve of *N. forsteri* does not resemble the features evidenced by thin sections of Maleri coprolites either.

If the comparison between *N. forsteri* and *Ceratodus* is valid neither the size nor the internal

features of the Maleri coprolites provide a convincing evidence of their association with *Ceratodus*. If the Maleri coprolites cannot be associated with *Ceratodus* with any degree of confidence, what of the remaining fish? There is evidence of a spiral valve in the intestine of *X. decheni* (Williams 1972). Teeth of *Xenacanthus* are present in most of the Pennsylvanian and Permian localities where spiral coprolites have been found (Price 1927, Moran and Romer 1952, Romer 1958, Williams 1972). Although it therefore appears logical to associate the xenacanth with the spiral coprolites, three important factors suggest otherwise. These are: (1) frequency of occurrence, (2) anatomical features, and (3) size discrepancy. *X. indicus*, so far, is known from only two blocks of calcified skull cartilages, possibly representing two specimens. This is inconsistent with the abundance of spiral coprolites. It is possible, however, that isolated xenacanth teeth occur frequently in Maleri clays but have been missed because of their microscopic size. A similar situation has been mentioned by Stewart (1978, p. 14) in dealing with Kansas Permian xenacanth remains. Xenacanth fish have a spiral valve in the intestine whereas coprolites suggest a scroll valve. *X. indicus* is estimated to be about 1.2 m long. The spiral coprolites from Maleri appear to be too small to represent 'fossilized intestinal contents' of this robust xenacanth, though no data are available on relative size. Thus the evidence to associate the xenacanth fish with spiral coprolites is inconclusive.

Since some palaeoniscoids (e.g. *Palaeoniscus*) and the extant holosteans have a spiral valve in the intestine, the possibility that the subholostean was the producer of the spiral coprolites appears to be quite strong. However, the Maleri subholostean is as yet undescribed and in any case its estimated size is almost the same as most of the coprolites. Thus the possibility of their association cannot be seriously considered.

The interpretation of the Maleri coprolites is still far from satisfactory and a number of tantalizing problems remain. Ash (1978) suggested that the upper Triassic (Chinle) spiral coprolites were probably produced by several different unspecified groups and sizes of animals. There is equivocal evidence that the Maleri spiral coprolites are either preserved intestines (enterospirae), intestinal contents, or faeces of known Maleri fauna. It is also possible, however, that they were produced by some unknown faunal element or represent the body of an as yet undetermined faunal element in the Maleri beds.

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THE PLEISTOCENE RODENT *ALTERODON MAJOR* AND THE MAMMALIAN BIOGEOGRAPHY OF JAMAICA

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ABSTRACT. The putative Jamaican octodontid rodent *Alterodon major* is based on a single cheek tooth. Restudy of this specimen indicates that it is probably incomplete, and that it is much more likely to represent a heptaxodontid than an octodontid. If this inference is correct, then there is no longer any reason to believe that there was an independent octodontid invasion of Jamaica. Although this clears up one biogeographical puzzle, no new light is shed thereby on the origins and dispersals of Caribbean land mammals. Jamaica occupies a key position in island-hopping models, but virtually nothing is known of the mammalian palaeontology of this island. Further investigations are clearly indicated.

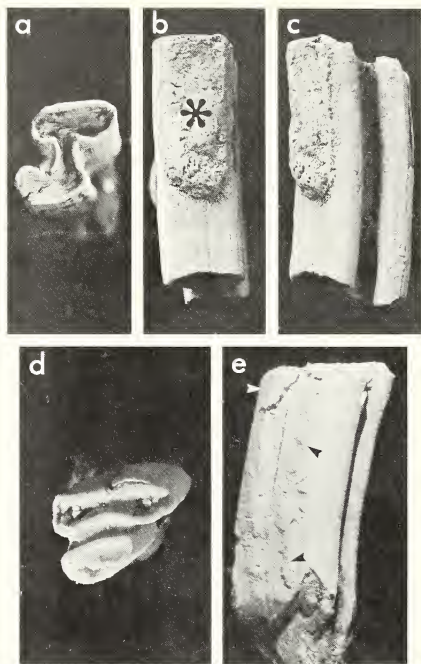
ALTERODON MAJOR, a fossil hystricognath rodent usually assigned to Octodontidae (e.g. Anthony 1926; Winge 1941; Simpson 1945; Landry 1957), is based on a single cheek tooth recovered from a Jamaican cave breccia of presumed latest Pleistocene or Holocene age (Anthony MS, 1920). The presence of this rodent in the Greater Antilles is difficult to explain, since octodontids are otherwise restricted to the southern part of South America (Simpson 1956; Wood and Patterson 1959). If correctly allocated, this specimen has significant implications for current theories regarding the minimum number of separate invasions required to explain the composition of the Caribbean rodent fauna (Woods and Howland 1979).

In the course of other work each of us has had the opportunity to examine the type of *Alterodon*, and each of us has concluded that it does not represent an octodontid. Others (e.g. S. B. McDowell *vide* Simpson 1956) have reached the same conclusion, but no previous researcher has formally reassessed *Alterodon*'s validity or proper allocation. This we undertake here, together with a short reassessment of the mammalian biogeography of Jamaica.

Institutional abbreviations used in the text and figures are: AMNH (American Museum of Natural History), FSM (Florida State Museum), and NRCDC (Natural Resource Conservation Department, Ministry of Mining, Government of Jamaica).

ALLOCATION OF *ALTERODON MAJOR*

The holotype (AMNH 17638) of *Alterodon major* is anatomically simple, consisting of two unequal laminae united by a narrow bridge (text-fig. 1a-c). The occlusal surface is reminiscent of the numeral 8—hence Anthony's *nomen*, a strophe on the Greek for 'dumb-bell'. The cores of the laminae are dentine, and their enamel casing is continuous and uncomplicated. The pulp cavity of the tooth is exposed, indicating that the tooth was unrooted. In all of these details of construction AMNH 17638 is indeed superficially similar to the bilobate or bilaminar configurations characteristic of non-acaremyine octodontid cheek teeth, as Anthony asserted in his comparisons. However, his diagnosis cannot be accepted at face value, because the specimen is almost certainly incomplete. Anthony (1920, p. 475, fig. 4) illustrated, but did not comment on, a thick layer of cementum on an exposed surface of the type's larger lamina. This layer is roughened and damaged (text-fig. 1b, c), suggesting breakage and perhaps the loss of some substantial portion of the original tooth. How much was lost is of course uncertain, since the specimen is unique. However, the simplest explanation for the specimen's present appearance is that the tooth was originally composed of



TEXT-FIG. 1. Holotype (AMNH 17638) of *Alterodon major* (a, b, c), compared to an incomplete cheek tooth of a specimen (AMNH 108554) referred to *Clidomys parvus* (d, e). Views are a, d, occlusal; b, ?distal; and c, e, ?distolateral. Asterisk in b identifies cementum plaque; remnants of homologous plaque can be seen on *C. parvus* specimen (e, pointers). Other specimens of latter tooth possess three laminae. About $3.5 \times$.

several laminae, welded together by plaques of interstitial cementum. One or more of these laminae spalled off during the deposition process, thereby considerably altering the tooth's size and complexity. Multilaminar, cementum-bound cheek teeth are moderately common in Hystricognathi; depending upon species, such teeth may consist of three to thirty (or more) lamina-plaque units. But teeth of this sort are *not* found among known Octodontidae, with the single egregious example of *Alterodon*. If we are correct in our interpretation that this tooth is incomplete, then the basis for Anthony's allocation disappears and *Alterodon*'s proper taxonomic placement must be sought elsewhere.

We tried but failed to find a match for AMNH 17638 among extant and extinct hystricognath genera restricted to South and Central America. Fugitive resemblances to non-Antillean families with multilaminar teeth (e.g. members of Dinomyidae) were neither detailed enough nor numerous

enough to warrant serious consideration. Families presently or previously resident in the Caribbean (Table 1) are obvious choices for *Alterodon*'s source, but of these the only likely candidates are Capromyidae and Heptaxodontidae. The native capromyid of Jamaica is *Geocapromys* (coney or hutia), but the sole specimen of *Alterodon* is clearly too large and too morphologically divergent to represent that genus. The same conclusion applies to other capromyid genera distributed elsewhere in the Caribbean. *Alterodon* is, however, well within the size range of heptaxodontids, and two facts justify the conclusion that *Alterodon* is almost certainly a member of this latter group even though precise allocation remains elusive.

TABLE 1. Distributions of Land Mammal Families in the Greater Antilles*

	Jamaica	Cuba	Hispaniola	Puerto Rico
Solenodontidae		×	×	
Nesophontidae		×	×	×
Cebidae			×	
Atelidae	×			
Megalonychidae		×	×	×
Cricetidae	×			
Heptaxodontidae	×		×	×
Capromyidae	×	×	×	×
	4-5	8-10	11-12	5-7

* The status and affiliation of several Antillean genera are currently in doubt and the subject of some disagreement among ourselves. In constructing this table, decisions about family limits and contents were made by consensus, in the following manner. Solenodontidae, Nesophontidae, Megalonychidae, and Cricetidae are defined and distributed as in Simpson's (1956) paper. *Xenothrix* (Williams and Koopman 1952) is a pitheciine atelid according to Rosenberger's (1977) cladogeny, and not a cebid unless one chooses to group all New World monkeys in a single family. Cebidae *sensu stricto*, however, do occur in Hispaniola (Rimoli 1977; MacPhee and Woods 1982). Heptaxodontidae may not be monophyletic (Ray 1964, 1965), but pending further study we retain the accepted form of this family (and include *Quemisia*). The coypus and the spiny rats of the Caribbean are usually regarded as being members of separate families (Capromyidae and Echimyidae respectively), but Woods (in press) argues that they are in fact sister groups and should probably be included in a single family (Capromyidae). The sister group of this latter taxon consists of non-Antillean echimyids (i.e. those living in South America).

Precise generic counts are not feasible at this time; the stated ranges are probable maxima and minima. Historical introductions (e.g. *Herpestes* in Jamaica) are omitted.

First, no other putative octodontid fossil has been found at *Alterodon*'s type locality—Wallingford Roadside Cave—but heptaxodontids have, and in abundance. This is of some importance, because nothing else has come out of Wallingford except coney bones and the remains of various reptiles. (Wallingford Roadside Cave is, in fact, the type locality of all of Jamaica's nominal heptaxodontid species, and is the only site on the island where their remains are frequent in 'bone breccias'.) In a recent collecting trip one of us (R.D.E.M.) spent several days at Anthony's old excavations at Wallingford and freed about seventy fossils from the breccia coating the cave's walls. Not one of them proved to be allocatable to Octodontidae. We doubt that inadequate sample sizes can explain the lack of new material of *Alterodon*.

The second reason for suspecting that *Alterodon* is really a heptaxodontid is based on preferential fracturing patterns of rodent teeth. Heptaxodontid cheek teeth, which consist of three or four laminae completely separated by cementum plaques, tend to fracture cleanly at enamel-cementum boundaries. Teeth which do not consist of completely independent lamina-plaque units are more likely to crumble or to fracture raggedly when force is applied to a selected point. Signs of

damage are usually obvious in the second case, but may not be in the first. In museum collections of heptaxodontids one can find numerous examples of isolated whole laminae which retain patches of cementum on their mesial or distal surfaces (text-fig. 1*d, e*); the gross resemblance of these partial teeth to the *Alterodon* specimen is obvious. Without forcing the available evidence beyond its limits, the following series of conclusions seem justified: if AMNH 17638 is incomplete, *Alterodon* cannot be an octodontid; if the specimen does not represent some heretofore unknown group of New World rodents, *Alterodon* is probably a member of some radiation native to the Greater Antilles; and in view of the island and place of its discovery, membership most probably lies with Heptaxodontidae.

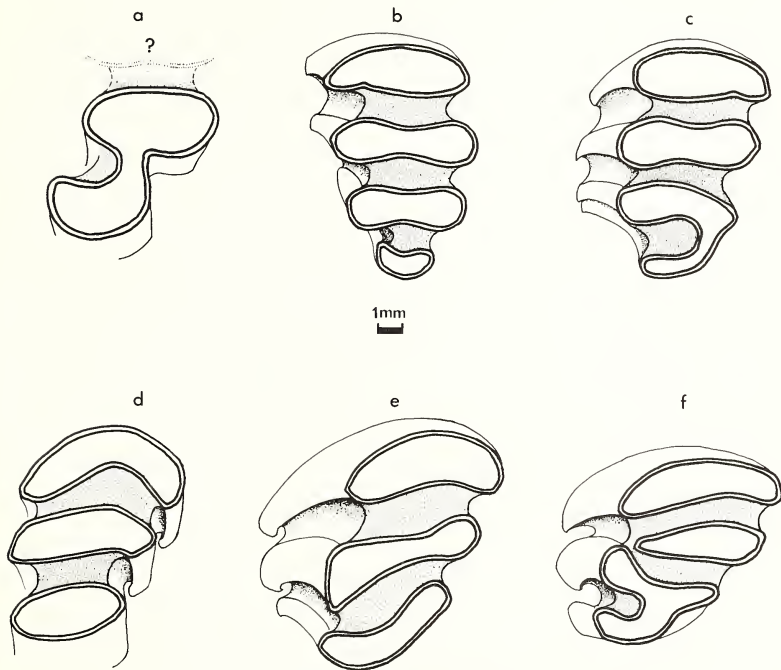
Although we adopt the view that *A. major* is a heptaxodontid, its condition is such that we cannot place it precisely within the group. The holotype may represent a distinct genus or species, or it may be no more than an individual variant of some other recognized taxon. In favour of the first option is the fact that no tooth or tooth fragment in the collections of the AMNH, FSM, or NRCD exactly conforms to AMNH 17638 (although some come close; see text-fig. 2). Supporting the second interpretation is the fact that reinvestigation (MacPhee, in prep.) of all available specimens of Jamaican heptaxodontids reveals that Anthony (1920) seriously misevaluated their within-group variability. Although there is considerable variation in size within the group, distributions are distinctly bimodal for most measurable traits, and there is no good reason to recognize more than two species (of one genus) in taxonomically partitioning the sample. (Anthony recognized four, which he distributed among three genera.) Pending proposed revision of Heptaxodontidae, it seems best to recognize *A. major* as an additional species, but with the caveat that it may represent no more than an individual variant of *Clidomys* (the genus name having page priority in Anthony [1920]). The resemblance of *Alterodon* to other heptaxodontids of the West Indies (Table 1) is no greater than one would expect in distant members of the same family, and there is no compelling reason to believe that *Alterodon* and *Clidomys* derive from different ancestries within Heptaxodontidae.

MAMMALIAN BIOGEOGRAPHY OF JAMAICA

The most obvious effect of including *Alterodon* within Heptaxodontidae is that Jamaica's known faunal diversity, already meagre, is reduced by one family. The non-chiropteran mammals compose a truly depauperate brigade—one species each of Capromyidae (*Geocapromys brownii*), Cricetidae (*Oryzomys antillarum*), and Atelidae (*Xenothrix mcgregori*), and an indefinite but surely small number of heptaxodontids. Exclusion of Octodontidae from this list leaves Jamaica with the smallest range of land mammals of any of the Greater Antilles (Table 1).

Unfortunately, recognition of the probable affinities of *A. major* does not shed any new light on the vexed question of the origins and subsequent fate of the Antillean land mammal fauna. Most students still prefer the dispersionist argument espoused by Matthew (1918), Darlington (1938), Simpson (1956), Pregill (1981), and others, which specifies that the distribution of Caribbean mammals (and many other organisms) can be most parsimoniously explained as the concatenation of many independent immigration events. This explanation assumes that Antillean populations were founded exclusively by waifs, which were able to disperse from circumjacent mainlands or previously occupied islands by riding on rafts of natural vegetation and suchlike vehicles (e.g. palm-frond 'boats'). Dispersal mechanisms of this sort are rejected as improbable by proponents of the vicariance hypothesis of Caribbean biogeography (Rosen 1976, 1978; see also general discussion in Nelson and Rosen 1981). Vicarists, however, propose the no less improbable thesis that the big islands have drifted out into the Caribbean Sea carrying nearly their entire native fauna with them. While it is likely that plate motions have indeed affected the relative positions of these islands, the scope of these movements appears to have been much less than required by the vicarist scenario (Pregill 1981). In any event, since the islands have been in approximately their present locations for most of the Cenozoic, the pertinence of plate tectonics to understanding the origins of Caribbean mammals appears to be slight.

Jamaica's role (if any) in ancient faunal movements within the West Indies is quite uncertain. In its faunal composition Jamaica differs sharply from Cuba, Hispaniola, and Puerto Rico in lacking insectivores and sloths (Table 1). Its apparent biotic isolation from the other Greater Antilles is further emphasized by the distinctiveness of *Xenothrix* and *Clidomys* (and *Alterodon*) within their respective families, which in turn implies lengthy separations from their supposed Caribbean-Neotropical relatives (Rosenberger 1977; MacPhee and Woods 1982). Indeed, as regards Jamaican



TEXT-FIG. 2. Comparison of occlusal surface organization in *Alterodon* (a, AMNH 17638) and selected Jamaican heptaxodontid teeth (semischematic). One possible match for the *Alterodon* holotype is the tetralaminar tooth illustrated in b (AMNH 108557, *Clidomys parvus*), which Anthony (1920) regarded as the ?M³ of *Clidomys* sp. The two distal laminae of the putative M³ (no *in situ* specimens are known) are continuous in some specimens of this tooth (e.g. c, AMNH 17635, holotype of '*Spirodonomys jamaicensis*' Anthony 1920). An alternative match is M₃ of *Clidomys* sp. (e.g. d, AMNH 108543), although no (other) examples of laminar bridging at this locus have been found. Another possibility is the permanent P₄, often highly variable in hystricognath species. Among hepatoxodontids a simple trilaminar configuration is typical for P₄ (e.g. e, AMNH 108556), but more elaborate versions are also found (f, FSM 27438). Non-Jamaican heptaxodontids exhibit premolar replacement, and it is likely that the same was true for the Jamaican forms. We cannot exclude the possibility that AMNH 17638 is a *deciduous* premolar of *Clidomys* (which may account for its rarity in existing collections).

mammals (other than bats), the only native genus found on at least one other island is *Geocapromys* (in Cuba and several offshore islands). Since the original centre of capromyid dispersion was probably in the eastern rather than the western Caribbean (Woods, in press), *Geocapromys* in all likelihood crossed into Jamaica from Cuba rather than vice versa. These points could be interpreted as an indication that Jamaica has been a faunal backwater which received only a small handful of land mammal immigrants during the late Cenozoic, and that most dispersal events and interchanges occurred among the islands to the north and east. However, another possibility exists. Jamaica is advantageously placed for receiving immigrants from Central America and northern South America, and despite vicarist reservations it is not unreasonable to believe that this geographical proximity to major land masses may have played some role in trans-Caribbean dispersals. Although Jamaica is now separated by a wide sea barrier from Central America, in the mid-Oligocene a major depression in sea-level (Vail *et al.* 1978) may have exposed parts of the Nicaraguan Plateau. Since the Plateau's eastern boundary lies off western Jamaica, only a short sea journey may have separated immigrating land mammals from their initial Antillean landfall. Other rafting events would still have to be invoked to account for the known distributions of primates, sloths, insectivores, and rodents in the northern and eastern islands, since Jamaica has been separated from Cuba and Hispaniola by deep (although not necessarily wide) troughs throughout the Cenozoic (Arden 1975).

Although attractive in some respects, this version of the dispersionist argument lacks the benefit of hard evidence: no one has ever found remains of these ancient transients in Jamaica. But since no one other than Anthony has made much of an effort to look for them, it remains to be seen whether this objection is fatal. The time spanned by the known mammal fauna of Jamaica is probably not more than a few tens of thousands of years, if bone-based dates of similar faunas from other locations in the Greater Antilles are a good guide (cf. Pregill 1981; MacPhee and Woods 1982). Yet sections of Jamaica have probably been positive for at least the latter half of the Cenozoic (Arden 1975; Robinson *et al.* 1977), and therefore potentially available for occupation. The extinct mammals of Jamaica must have had antecedents, and further work on the island is strongly indicated. Some major biogeographical puzzles may thereby be solved.

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TEETH OF A NEW NEOSELACHIAN SHARK FROM THE BRITISH LOWER JURASSIC

by C. J. DUFFIN and D. J. WARD

ABSTRACT. Neoselachian sharks' teeth from the lower Jurassic of Lyme Regis, Dorset, are described and assigned to *Agaleus dorsetensis* gen. et sp. nov. The teeth are large, and have a robust central cusp, one pair of lateral cusplets, and a prominent basal flange. Longitudinal ridges are present on the labial crown shoulder, and the root has a strong labial buttress. The vascularization is hemiaulacorhize. Comparison with the teeth of Recent and fossil neoselachians indicates that *Agaleus* is a benthonic orectolobiform galeomorph.

THE lower Jurassic limestones and shales of the Lyme Regis succession on the Dorset coast have long been famous for yielding whole and fragmentary vertebrate remains (Lang 1924). Amongst this vertebrate fauna, fossil elasmobranchs are represented by hybodontiforms (*Acrodus anningiae*, *A. nobilis*, *Hybodus varicostatus*, *H. delabechei*, *H. medius*, *H. reticulatus*) and a few specimens of presumed (on the basis of enameloid ultrastructure, Reif 1974) neoselachians (*Palaeospinax priscus*).

Neoselachian sharks are those belonging to the level of organization of Recent species. The fossil record of this group is well represented in the late Cretaceous and Tertiary but sporadic in the remainder of the Mesozoic. The best-known specimens have been recovered from the fine-grained limestones of the Bavarian Tithonian (upper Jurassic) in south-west Germany. Here, the squalomorphs are represented by *Notidanus*, the batoids by *Belemnobatis* and *Asterodermus*, the squatinomorphs by *Squatina*, and the galeomorphs by several orectolobids (*Corysodon*, *Phorcynis*, *Orectolobus*), a heterodontid (*Heterodontus*), carcharhiniforms (*Palaeoscyllium*, *Pristiurus*), and what may be a lamniform (*Palaeocarcharias*).

Few neoselachians are known prior to the Kimmeridgian: *Palaeospinax* has already been mentioned from the lower Lias; the remainder comprise mostly isolated teeth and fin spines of neoselachians of problematic ordinal affinity from late Triassic deposits (Duffin 1981), including *Raineria* Osswald 1928, *Nemacanthus* Agassiz 1837, *?Pseudodalatias* (Sykes 1971), *Hueneichthys* Reif 1977, *Reifia* Duffin 1980, and *Vallisia* Duffin 1982. In addition, Duffin and Ward (1983) have reported neoselachian sharks' teeth from the early Carboniferous of Britain and the Permian of the U.S.A. (*Anachronistes* spp.). Thus, considerable gaps exist in our knowledge of the early history of the neoselachians. One of the more important of these is that represented by the poorly sampled lower Jurassic deposits. In sediments of this age we should expect to find evidence of the early members of extant neoselachian orders and families. The purpose of this paper is to begin such a study with the description of a new neoselachian shark from the Blue Lias (early Jurassic) of Lyme Regis, England.

SYSTEMATIC PALAEONTOLOGY

Class CHONDRICHTHYES
Subclass ELASMOBRANCHII
Cohort NEOSELACHII
Superorder GALEOMORPHII
Order ORECTOLOBIFORMES
Family *incertae sedis*
Genus *Agaleus* gen. nov.

Derivation of name. A genus of presumed galeomorph shark named in honour of Mr. Andrew Gale.

Diagnosis. Genus known only by large (up to 7 mm high) isolated teeth. The central cusp is large, lingually inclined, and flanked by one lateral cusplet on each side. The lateral blades are pronounced and the basal flange well developed and expanded basally. A series of horizontal ridges is present around the whole tooth at and below the crown shoulder. The ridges vary in length, and divide and converge on each other. Short vertical striations may arise from certain horizontal ridges. The horizontal ridges are particularly common along the crown shoulders of the lateral blades. The crown/root junction is deeply incised around the whole tooth. The root is deep, and has a V-shaped basal face and hemiaulacorhize vascularization. Up to two pairs of lateral canals may be developed high on the labial and lingual root faces, and up to three median canals may be present. A pronounced labial buttress of the root is present beneath the basal flange.

Agaleus dorsetensis sp. nov.

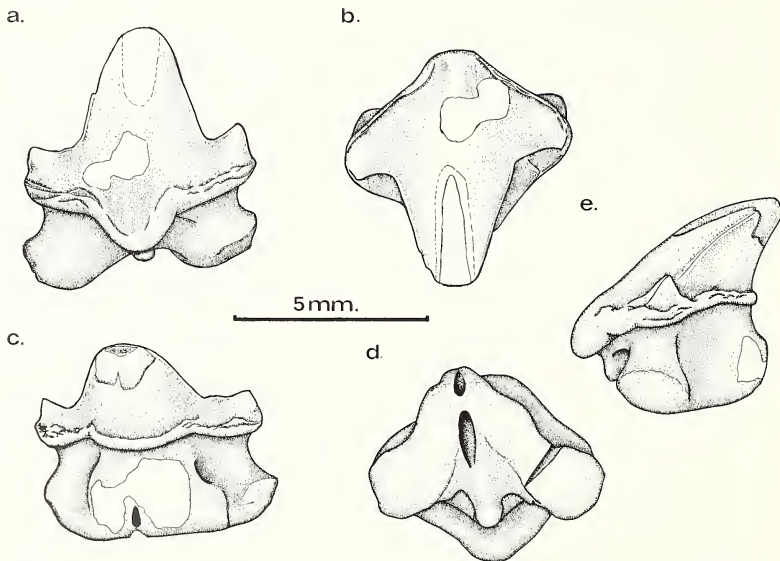
Text-figs. 1a-e, 3a-e

Diagnosis. As for genus.

Derivation of name. After Dorset, the county in which the teeth were found.

Holotype. P.60788 BM(NH), a complete tooth (text-figs. 1a-e), collected by Mr. A. Gale from a fallen block below Church Cliff, Lyme Regis.

Other Material. Two teeth; P.60789 BM(NH), an isolated crown, collected by Mr. D. Kemp in 1975 from a fallen block below Church Cliff, Lyme Regis; GSM 117084 (text-fig. 3), complete tooth, collector unknown.



TEXT-FIG. 1. Holotype of *Agaleus dorsetensis* (BM(NH) P.60788) from the lower Jurassic of Lyme Regis, Dorset. a, labial view; b, occlusal view; c, lingual view; d, basal view; e, lateral view.

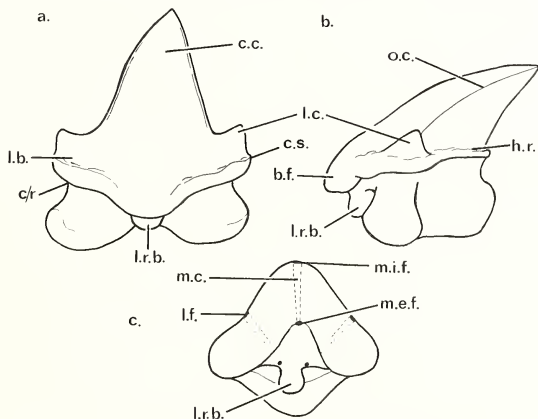
Age. P.60788 and P.60789 are from the Blue Lias, ?Lower Sinemurian, lower Jurassic. GSM 117084 is labelled 'Lower Lias' only.

Locality. P.60788 and P. 60789 are from Church Cliff, Lyme Regis, Dorset, England. ST345925. The locality for GSM 117084 is unknown.

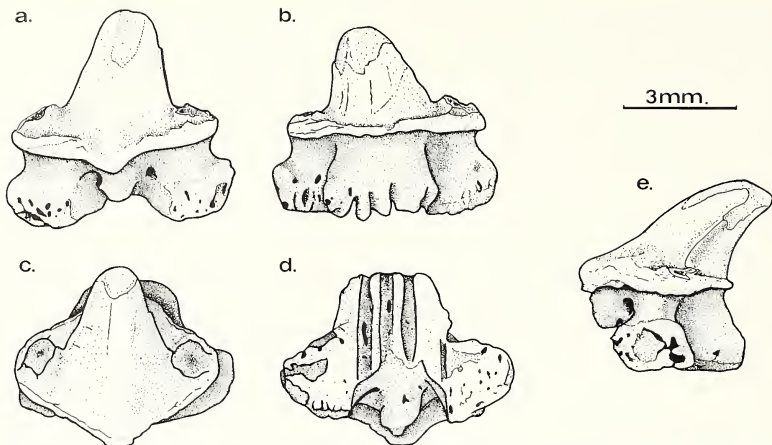
Description of the holotype. The holotype (text-fig. 1*a-e*) is a complete tooth sustaining some antemortem wear, and measuring 6.9 mm high (crown apex to root base), 6 mm long (mesiodistally), and 6.5 mm wide (labiolingually).

The crown is robust and comprises a central lingually inclined cusp with circular cross-section. The central cusp (c.c., text-fig. 2) is flanked on either side by one lateral cusplet (l.c.) which is less than one-sixth of the height of the central cusp (text-fig. 1*a, c*). The lateral blades (l.b.) of the tooth are well developed and there is a prominent basally projecting basal flange (b.f.) (text-fig. 1*a, b, e*). The central cusp sustains antemortem wear at the apex, along the top of the labial face, and toward the basal flange (text-fig. 1*a, c, e*). The basal flange possesses two depressions labially, separated by a low vertical ridge which begins to ascend the central cusp (text-fig. 1*a*). The labial face is shorter and concave (text-fig. 1*e*). A mesiodistal longitudinal ridge, the occlusal crest (o.c.), runs the length of the crown and passes through the apices of the cusps, forming cutting edges. The top of the crown shoulder is somewhat expanded around the whole of the tooth and possesses a series of horizontal ridges (h.r.) (text-fig. 1*a-c, e*). The ridge at the top of the crown shoulder is the most prominent, but is not continuous around the tooth. It contains many gaps, and short vertical ridges arise from it. Further longitudinal ridges are present below the crown shoulder, often broken and sometimes dividing or converging. These accessory ridges are more pronounced on the labial and lingual shoulders of the mesial and distal lateral blades (text-fig. 1*a, c*). There is no further ornament.

The crown/root junction (c/r) is deeply incised around the whole tooth and particularly beneath the basal flange labially. The root is deep (just under half of the total tooth height) and has a V-shaped basal face whose apex is directed lingually (text-fig. 1*d*). The lateral arms of the V are expanded labially. The vascularization is hemiaulacorhize; a median canal (m.c.) is partially roofed and connects a medio-internal (m.i.f.) and medio-external foramen (m.e.f.). There is one pair of lateral internal and external foramina (l.f.)



TEXT-FIG. 2. Diagram to illustrate technical descriptive terms used in the text. Tooth in *a*, labial view; *b*, lateral view; *c*, basal view. c.c. central cusp; l.c. later cusplet; l.b. lateral blade; b.f., basal flange; o.c., occlusal crest; h.r., longitudinal ridge; c/r, crown/root junction; m.c., median canal; m.i.f., medio-internal foramen; m.e.f., medio-external foramen; l.f., lateral foramen; l.r.b., labial root buttress; c.s., crown shoulder.



TEXT-FIG. 3. Tooth of *Agaleus dorsetensis* (GSM 117084) in a, labial view; b, lingual view; c, occlusal view; d, basal view; e, lateral view.

situated half-way up the labial and lingual root walls (text-fig. 1c, e). Just beneath the basal flange, a short but robust labial root buttress (l.r.b.) is developed, separating the two lateral labial foramina (text-fig. 1a, d, e).

Variation. P.60789 comprises an isolated crown, measuring 7 mm from central cusp apex to the base of the basal flange, and 5 mm mesiodistally. The specimen agrees with the general morphology of the holotype and has sustained less antemortem wear. The basal expansion of the basal flange is not quite so pronounced as in the holotype, and longitudinal ridges at the crown shoulder are fewer in number and mostly restricted to the lingual side. Also, there are isolated vertical ridges ascending the mesial and distal edges of the central cusp and lateral cusplets for a short distance (1.5 mm).

GSM 117084 (text-fig. 3a-e) is identical to the holotype in the structure of the crown and distribution of antemortem wear. The lateral cusplets have been removed by post-mortem abrasion. The overall root morphology is as for the holotype, with the exception of the vascularization. The labial extremities of the lateral root prongs and the lingual apex of the V-shaped flat basal root face are markedly expanded. The basal root face has been somewhat eroded (text-fig. 2d). Three open median canals are present crossing the basal root face labiolingually. A fourth median canal of identical orientation is present in a more lateral position.

DISCUSSION

Agaleus dorsetensis possesses a well-differentiated crown and root and hemiaulacorhizoid root vascularization (Casier 1947). This combination of characters exists only in the neoselachian sharks (Duffin and Ward 1983). Although a thick enameloid layer is present in *Agaleus*, its ultrastructure has not been investigated owing to the scarcity of specimens.

The neoselachians are divided into four superordinal groups (Compagno 1973): Batoidea, Squatinomorphii, Squalomorphii, and Galeomorphii, all of which are represented in Jurassic deposits. Squalomorph sharks usually possess teeth which are strongly labiolingually compressed, acting as scissor blades (e.g. *Isistius*) with an anaulacorhizoid vascularization. Batoid teeth are low-crowned, usually non-cuspidate, with anaulacorhizoid or holaulacorhizoid root vascularization. The hemiaulacorhizoid root vascularization shown by *Agaleus* is restricted to galeomorph and squatinomorph sharks (Table 1).

TABLE 1. Comparison of the teeth of *Agaleus dorsetensis* with those of Recent and fossil neoselachians. +, character present; -, character absent; H, hemiaulacorhize vascularization; Ho, holaulacorhizoid vascularization; A, anaulacorhizoid vascularization.

	<i>Agaleus dorsetensis</i>	Squalomorphs	Batoids	<i>Squatina</i>	<i>Heterodontus</i>	Lamniforms	Carcharhiniforms	<i>Parascyllium</i>	<i>Cirrhoscyllium</i>	<i>Hemiscyllium</i>	<i>Chiloscyllium</i>	<i>Synchlisma</i>	<i>Eostegostoma</i>
CROWN CHARACTERS													
Basal flange	+	+	-	+	+	-	-	+	-	-	-	-	+
Lingual apron	+	+	-	-	-	-	-	-	-	+	+	+	+
Lateral cusplets	1	0-1	0	0	0-4	0-2	0-4	1	1	0-1	0-1	0-1	1
Longitudinal ridge	+	-	-	-	-	-	-	-	-	-	-	-	-
ROOT CHARACTERS													
Vascularization	H	A	Ho/A	H	H	Ho	Ho/A	Ho	H	H	H	H	H
Root buttress	+	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Stegostoma</i>	<i>Rhinodon</i>	<i>Palaeorhynchodon</i>	<i>Ginglymostoma</i>	<i>Protoginglymostoma</i>	<i>Nebrius</i>	<i>Eucrossorhinus</i>	<i>Orectolobus</i>	<i>Brachaelurus</i>	<i>Squatirhina</i>	<i>Anachronistes</i>	<i>Doracodus</i>	<i>Almascyllium</i>
CROWN CHARACTERS													
Basal flange	-	+	+	+	-	+	+	+	+	+	+	-	+
Lingual apron	+	+	+	+	+	+	+	+	+	+	+	-	+
Lateral cusplets	1	0	0-1	2-5	1-3	2-12	0	0	1	0-1	1	1	1
Longitudinal ridge	-	-	-	-	-	-	-	-	-	-	+	+	+
ROOT CHARACTERS													
Vascularization	H/Ho	H	H	H	H	H	Ho/H	H	H	Ho	H	?	H
Root buttress	-	-	-	-	-	-	-	-	-	-	+	?	-

Our knowledge of squatinomorph sharks' teeth is restricted to the single extant genus *Squatina*, and a small number of fossil species. The general tooth morphology comprises an elongate central cusp flanked by non-cuspidate lateral blades. *Agaleus* shares the possession of a hemiaulacorhizoid root with *Squatina*, and the presence of a strong labial flange at the base of the crown. It differs markedly in crown architecture, however, having strong lateral cusplets flanking a low central cusp.

Among Galeomorphii, hemiaulacorhizoid root vascularization is seen only in *Heterodontus* and the orectolobiforms (Table 1). The dentition of mature *Heterodontus* shows strong monognathic heterodonty in which only the anterior teeth are cuspidate; the lateral teeth form a crushing pavement. Also, only juvenile *Heterodontus* show the development of a basal flange (Reif 1976 figs. 23, 24); a small pair of lappets overhangs the crown root junction in adult anterior teeth (Reif 1976, fig. 23).

The basal flange in *Agaleus* is strongly developed, a feature seen in the teeth of a number of orectolobid genera (Table 1). *Agaleus* combines this feature with a single pair of lateral cusplets on the crown, a combination of features seen in the teeth of *Brachaelurus* amongst extant orectolobid sharks, and *Mesiteia* amongst fossil species. Thus the teeth of *Agaleus* superficially resemble those of *Brachaelurus* and *Mesiteia* most closely among orectolobids. *Mesiteia* is recorded from the Upper Cretaceous of Lebanon (Cappetta 1980) and the U.S.A. (Estes 1964, Cappetta 1973, Herman 1977). The extant genus *Brachaelurus* has been cited from the Turonian (upper Cretaceous) of South Dakota, U.S.A. (Cappetta 1973).

Teeth of *Agaleus* differ from those of all extant orectolobid genera, however, in possessing a labial root buttress which underlies the basal flange of the crown. This feature is known only in the Carboniferous and Permian genus *Anachronistes* (Duffin and Ward 1983), a presumed neoselachian of doubtful ordinal status. In addition, *Agaleus* possess well-defined horizontal ridges on the labial and lingual crown shoulders. This feature is not present in any Recent sharks tooth, to our knowledge. Amongst fossil neoselachians, it is weakly developed in *Anachronistes*. The problematic genus *Doratodus* (Duffin 1981) has a simpler horizontal ridge on the labial and lateral crown shoulders (Table 1).

The teeth of *Agaleus* are larger than those of any extant orectolobiform genera excepting *Nebrius* and *Ginglymostoma*. The labial buttress of the root may indeed have been instrumental in adding extra structural advantage to the crown during occlusion. We assume from the tooth shape and antemortem wear that *Agaleus* was of benthonic habit and durophagous diet, in common with most orectolobid species.

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TETRAMERIC CRINOID COLUMNALS FROM THE ORDOVICIAN OF WALES

by S. K. DONOVAN

ABSTRACT. *Colpodecrinus forbesi* sp. nov. is founded on the evidence of unusual tetrameric crinoid columnals similar to those of *C. quadrifidus* Sprinkle and Kolata. The columnals of *C. forbesi* have quadrangular lumina, either tetrastellate or square, whereas those of *C. quadrifidus* are tetralobate.

THE echinoderm endoskeleton is constructed of numerous ossicles that are usually dispersed after death and which are sometimes sufficiently distinct to be of stratigraphic value. Such dissociated plates can sometimes be related to better known taxa based on whole specimens (e.g. see Donovan and Paul 1982). Although the majority of dissociated crinoid columnals lack distinctive features enabling more than a very general identification, some are sufficiently unique to be of some stratigraphic value (e.g. Rasmussen 1961). However, even columnals of a particular pelmatozoan group which appear to be extremely distinctive may prove to be homeomorphic with those of other stems (Broadhead and Strimple 1977).

Forbes (1848, p. 522) mentioned and illustrated an unusual echinoderm fossil collected by officers of the Geological Survey in North Wales during 1847 (text-fig. 1). This specimen is most remarkable in having fourfold symmetry with a definite suture between each lobe. Forbes tentatively interpreted this as the base of the theca of an unidentified cystidean. It is reinterpreted here as the external mould of a crinoid columnal of an unusual type which closely resembles the columnals of the species *Colpodecrinus quadrifidus* Sprinkle and Kolata, 1982. The almost unique tetrameric division of each columnal into four individual calcite plates (meres) makes the generic identification possible. The only other crinoid to possess a tetrameric stem is the lower Arenig species *Ramseyocrinus cambriensis* (Hicks) (Bates 1968). However, *Ramseyocrinus* has a lobate stem whereas *Colpodecrinus* columnals are almost circular (text-figs. 1A, 2A, B, C).

Terminology used in this paper follows Ubaghs (1978).

SYSTEMATIC PALAEONTOLOGY

Class CRINOIDEA J. S. Miller, 1824

Subclass CAMERATA Wachsmuth and Springer, 1881

?Order MONOBATHRIDA Moore and Laudon, 1943

Family COLPODECRINIDAE Sprinkle and Kolata, 1982

Genus *Colpodecrinus* Sprinkle and Kolata, 1982

Type species. *C. quadrifidus* Sprinkle and Kolata, 1982.

Diagnosis of stem. Stem tetragonal, heteromorphic, tetramere lobes aligned with infrabasal centres, lumen lobes sutural.

Colpodocrinus forbesi sp. nov.

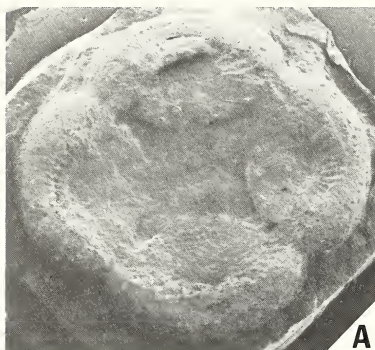
Text-figs. 1, 2A, B, D

v. 1848 Incertae sedis; Forbes, p. 522, pl. 23, fig. 14.

Derivation of name. After Professor Edward Forbes, who first figured the holotype specimen.

Diagnosis. A species of *Colpodocrinus* known from columnals only. Lumen tetragonal, with sharp angles; epifacet (latus) strongly convex.

Material. Forbes's original specimen, an external mould with no counterpart, is now registered as Institute of Geological Sciences GSM 48379 and is designated as the holotype. A second, poorly preserved specimen (British Museum (Natural History) E68627) has been collected by Dr. D. K. Wright of Kingston Polytechnic (text-fig. 2A, B). This paratype differs from the holotype in having fewer, coarser crenellae, a broader crenularium, and a square lumen.



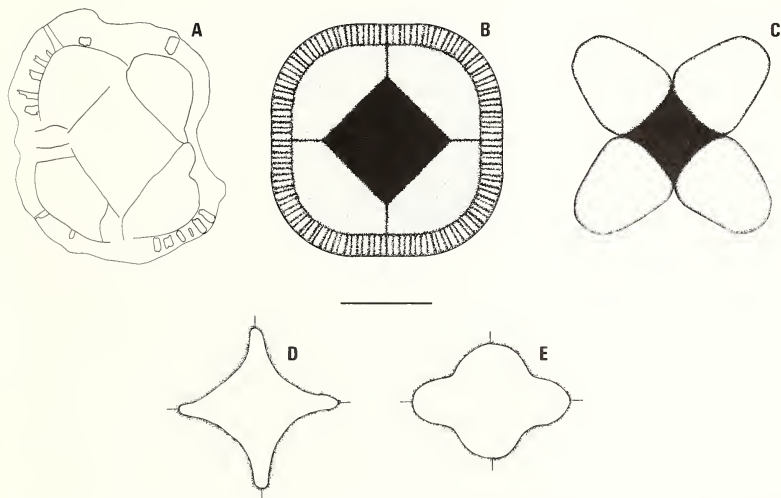
TEXT-FIG. 1A, B. Latex cast of the holotype of *Colpodocrinus forbesi* sp. nov., IGS GSM48379. SEM photographs. A, articular facet. B, oblique view to illustrate the epifacet curvature. Both $\times 8$.

Horizon and locality. Forbes (1848) merely described the holotype as being from the 'Silurian' (i.e. including the Ordovician) of North Wales. The specimen label states 'Caradoc. 2 miles W of YspuTTY Evans'. The old series Geological Survey one-inch map 75 NE has a patch of Bala Limestone at National Grid Reference SH 818 500 which apparently corresponds to this locality (S. P. Tunnicliff, pers. comm.). The paratype specimen is from the Glanrafon Beds at SH 7612 5104, south-east of Dolwyddelan, which Dr. Wright regards as being of Soudleyan age (pers. comm.).

Description. Columnal rounded, almost circular, composed of tetrameres. Lumen large, tetrastellate to square, occupying less than half the area of the facet, angles corresponding to the meric sutures of the columnal. Areola of each tetramere large, slightly depressed, triangular to lozenge-like in outline. Marginal symplexy, approximately fifteen to twenty-four crenellae per mere. Epifacet convex, semicircular in outline.

Discussion. The lumina of columnals of *C. quadrifidus* are orientated with the angles corresponding to the meric sutures of the stem. The lumen angles are well rounded with the lumen sides slightly infolded to give a petaloid appearance (text-fig. 2E). This differs from *C. forbesi*, which has strongly angular corners to the lumen (text-figs. 1A, 2A, B, D).

Ubaghs (1978) states that, apart from the unusual camerate genus *Cleioocrinus*, pentameric (quinquepartite) stems are limited to the inadunate crinoids. In addition, there are two rhombiferan cystoid genera with pentameric columnals, *Caryocystites* (Bockelie 1982) and *Echinospaerites* (Barrande 1887; Bockelie 1981). Similarly, until the description of *Colpodeocrinus*, the only crinoid known to have a tetrameric stem was the inadunate species *Ramseyocrinus cambriensis* (Hicks). The possession of a meric stem is undoubtedly a primitive feature but the relationship of *Colpodeocrinus* to more advanced camerate genera with tetragonal, holomeric (i.e. composed of a single plate) columnals, such as *Xenocrinus*, is obscure.



TEXT-FIG. 2A, B. The paratype of *Colpodeocrinus forbesi* sp. nov., BM(NH) E68627. A, camera lucida drawing of external mould of facet. B, reconstruction of facet. C, reconstruction of facet of *Ramseyocrinus cambriensis* (Hicks). D, E, lumina of *C. forbesi* (D) and *C. quadrifidus* (E). Scale bar represents 1 mm for A, B and 2.5 mm for C, D, E.

The ligamentary attachment between the meres of early crinoids seems to have been weak and their columnals are preserved either as pluricolumnals (due, presumably, to rapid burial) or as dissociated meres. For example, one specimen of *R. cambriensis* (NMW 29.308.G220) is a pluricolumnal that has started to disarticulate both between meres and at the quadquepartite sutures. The contact between meres increases in later crinoids such as *C. forbesi* (cf. text-fig. 2B and C), making them more likely to be preserved as single columnals.

C. quadrifidus is found only in the Upper Echinoderm Zone of the Upper Mountain Lake Member, Bromide Formation, Oklahoma, U.S.A. (Sprinkle and Kolata 1982), which correlates approximately with the upper Llandeilo-lower Caradoc of Europe (Williams *et al.* 1972; Fay and Graffham 1982). *C. forbesi*, based on the stratigraphic position of the paratype, is probably a slightly younger species.

The principal objection to erecting a new species based solely upon columnal evidence is the possibility that two or more crinoids may have identical stems. As has already been stressed, however, the columnals of *Colpodecrinus* are particularly unusual and such confusion is unlikely in the present example. It is also possible that we may be dealing with a previously unknown fragment from a species already described (in this case the type species). The longest attached stem fragment of *C. quadrifidus* is 16 mm long and the longest pluricolumnal 34 mm long. The articular facet morphology remains similar on both these stem fragments (Sprinkle and Kolata 1982). Although it is apparent that these stem fragments do not constitute the whole column, there is no evidence of a change in morphology in the available material. I conclude therefore that the differences in morphology, the spatial separation by the Iapetus Ocean, and the younger age of the Welsh specimens indicate that there are two distinct species of *Colpodecrinus*.

Two other crinoid species have been described from the Soudleyan stage in Britain, *Balacrinus basalis* (M'Coy) and *Iocrinus whitteryi* Ramsbottom, but neither is closely related to species from the Bromide Formation. Bates (1965, p. 357) has already discussed the division of the genus *Iocrinus* into two distinct geographical groups. The genus *Balacrinus* is monospecific. Additionally, a heterocrinid from below the Tramore Limestone (Ramsbottom 1961, p. 10) is of approximately the same age as the Upper Mountain Lake Member but no heterocrinids are known from the Bromide Formation. There is therefore little evidence for a general migration of Bromide crinoids to Britain.

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THE OLDEST KNOWN NOWAKIID (TENTACULITOIDEA)

by S. P. TUNNICLIFF

ABSTRACT. Specimens of the tentaculitoidean *Nowakia brevis* sp. nov. are described from the type locality of *Monograptus sedgwickii* (Portlock) in the Silurian of Pomeroy, Co. Tyrone, Ireland. This is the oldest known representative of the Nowakiidae, a family not known again in the fossil record until the early Devonian.

A NUMBER of small tentaculitoideans are present among the specimens collected by J. E. Portlock from the Silurian rocks of Pomeroy, Co. Tyrone (see Tunnicliff 1980), and are closely associated with the type specimens (Elles 1942) of the zone fossil *Monograptus sedgwickii* (Portlock). Portlock labelled some of these specimens as *Tentaculites brevis* (MS.) and recorded them as *Tentaculites*? (1843, p. 231, pl. 19, figs. 12a, b). In recent years, officers of the Geological Survey of Northern Ireland have collected further specimens. These are described here as *Nowakia brevis* sp. nov.

The *M. sedgwickii* horizon of the Limchill Beds of Pomeroy (Llandovery, Fronian, *M. sedgwickii* Zone) contains fine black mudstone associated with paler, grey, somewhat siltier beds (Fearnside *et al.* 1907, pp. 108, 109). The fauna is restricted to graptolites (Fearnside *et al.* 1907, p. 110 recorded five monograptid species plus *Climacograptus* and *Petalograptus*) and *N. brevis* with occasional bivalves (Pl. 84, figs. 15, 17, 18), a small atrypoid brachiopod (Pl. 84, fig. 16), indeterminate orthoconic nautiloid fragments, and *Aptychopsis*. Neither the graptolites nor the *Nowakia* show any preferred orientation, although graptolites are numerous and specimens several inches long are preserved. There is no evidence of bioturbation within the mudstones, which suggests an absence of benthic and burrowing organisms. A calm, deep-water, offshore palaeoenvironment above slowly accumulating sediment is inferred for *N. brevis*. The mode of life of the associated shells is open to speculation, but *Guerichia* Rzehak, 1910 (= *Karadjalia* Sadykov, 1962) (Pl. 84, fig. 15) is thought to have lived byssally attached to floating weed (House 1975, p. 481) and a similar habit is cited for certain brachiopods (Rudwick *in* Moore 1965, p. H201; Rudwick 1961, p. 475; 1970, p. 77). *N. brevis* was probably planktonic, associated with the free-floating monograptids, a mode of life suggested for *Nowakia* by most authorities (e.g. Fisher *in* Moore 1962, p. W104; Bouček 1964, p. 37; Lardeaux 1969, p. 90). Lardeaux (1969, p. 191) emphasized the similarity of mode of life and occurrence between the Dacryoconarida and monograptids. Hurst and Hewitt (1977, p. 151), while reviewing the facies distribution of the tentaculitid *Tentaculites*, mentioned that the Dacryoconarida occur abundantly in offshore facies in the Devonian while *Tentaculites* has not been recorded from graptolitic shales. Previously recorded Llandovery age tentaculitoideans are of the thicker-walled, bottom-dwelling *Tentaculites* type (see Hurst and Hewitt 1977, p. 163; Larsson 1979). The small, thin-walled, pelagic *N. brevis* represents an early development of nowakiid morphology and to some extent shared an ecological niche with the monograptids. It is, perhaps, significant that nowakiids are not known otherwise from the graptolitic Silurian and it is possible that there is a correlation between the decline of the graptolites in the Devonian and the flourishing of the nowakiids. If these specimens represent, as they seem to, a true *Nowakia*, the range of the genus and of the family Nowakiidae is extended considerably, the earliest previous records having been from the early Devonian (Gedinnian) (Bouček 1964, p. 58; Lardeaux 1969, p. 89). Some of the faunal elements with which *N. brevis* has been found appear morphologically similar to later, especially Devonian, forms which have been suggested to have been pelagic or epiplanktonic, in particular *Guerichia* and '*Leiorhynchus*'. Therefore, the Lime Hill fauna is an assemblage which includes early examples of morphological types which are not uncommon in Devonian rocks. The question remains: what happened to the nowakiids in the period between the Llandovery and the Devonian?

SYSTEMATIC PALAEONTOLOGY

The classification used in the *Treatise on Invertebrate Paleontology* Part W (Moore 1962) is adopted below class level. This is compatible with that of other authors (Bouček 1964; Lardeaux 1969; Larsson 1979). The material cited is in the collections of the Institute of Geological Sciences, London (IGS), and the Ulster Museum, Belfast (UM).

Order DACRYOCONARIDA Fisher, 1962
Family NOWAKIIDAE Bouček and Prantl, 1960
Genus *Nowakia* Gürich, 1896

Nowakia brevis sp. nov.

Pl. 84, figs. 1–14

v. 1843 *Tentaculites?* Portlock, p. 231, pl. 19, figs. 12a, b.

1890 *Tentaculites brevis* Portlock MS.; Tunnicliff, p. 91 [catalogue entry recording *brevis* as a *nomen nudum*].

Holotype. IGS NIE1238 (Pl. 84, fig. 10), the largest and most complete specimen known.

Material, horizon and locality. Individual specimens and groups of specimens on slabs from the Portlock Collection and recent Geological Survey of Northern Ireland collections: IGS GSM12664, 62652, 103609, NID2088, 2090, NIE1199, 1238, 1240, RU3863; and UM K4100, 4274, 4390–3. All from the Limehill Beds (Llandoverly, *M. sedgwickii* Zone) at Lime Hill, Pomeroy, Co. Tyrone. (Irish grid ref. H 6945 7390). All preserved as moulds, mostly external, but some (Pl. 84, fig. 7) showing internal detail.

Diagnosis. Medium-sized nowakiid with strong, fairly sharp rings, and fine transverse and longitudinal striae. Growth angle initially c. 30°, reducing to 20–25°.

Description. Straight, conical shell with a thin wall (c. 0.03 mm between rings and up to 0.1 mm at rings; Pl. 84, fig. 7). Initial stage tear-drop shaped (Pl. 84, figs. 5, 6, 10) and often slightly curved away from the main axis of the shell (Pl. 84, figs. 5, 10). The cross-section is assumed to have been circular in life. External surface marked by strong, fairly sharp rings (in the 2 to 3 mm interval, five specimens show 3½, 4, 4, 4, 5 rings, and in the 3 to 4 mm interval they show 3, 3½, 4, 4, 4 rings) and fine transverse striae (c. 2–4 per 0.1 mm) especially visible between rings; there are fine longitudinal striae (7–10 per mm) which increase in number distally, as new striae arise by insertion between existing ones (Pl. 84, fig. 8); I estimate a total of thirty to forty striae for the circumference of the available specimens. No evidence of internal septa. Internal surface undulating to correspond with the external relief (Pl. 84, fig. 7), but lacking the fine ornament. Maximum shell length seen 5.2 mm (Pl. 84, fig. 10); maximum width seen 2.2 mm (Pl. 84, figs. 3, 8). Juvenile growth angle c. 30°; mature growth angle typically 20–25°. Most specimens show some distortion, usually shell collapse evinced by a sub-median longitudinal crack (Pl. 84, figs. 2, 3, 6).

EXPLANATION OF PLATE 84

Figs. 1–14. *Nowakia brevis* sp. nov. All latex casts; 1–10, 13–14, × 10; 11, 12, × 5. 1, IGS GSM62652. 2, IGS RU3863. 3, IGS GSM12664. 4, IGS NIE1240. 5, IGS GSM12664. 6, IGS NID2088. 7, IGS NIE1199. 8, UM K4392. 9, IGS GSM62652. 10, IGS NIE1238, holotype. 11, IGS GSM12664, two specimens closely associated with the lectotype of *Monograptus sedgwickii* (Portlock). 12, UM K4390, a group showing no obvious orientation. 13, IGS GSM12664. 14, IGS NIE1199.

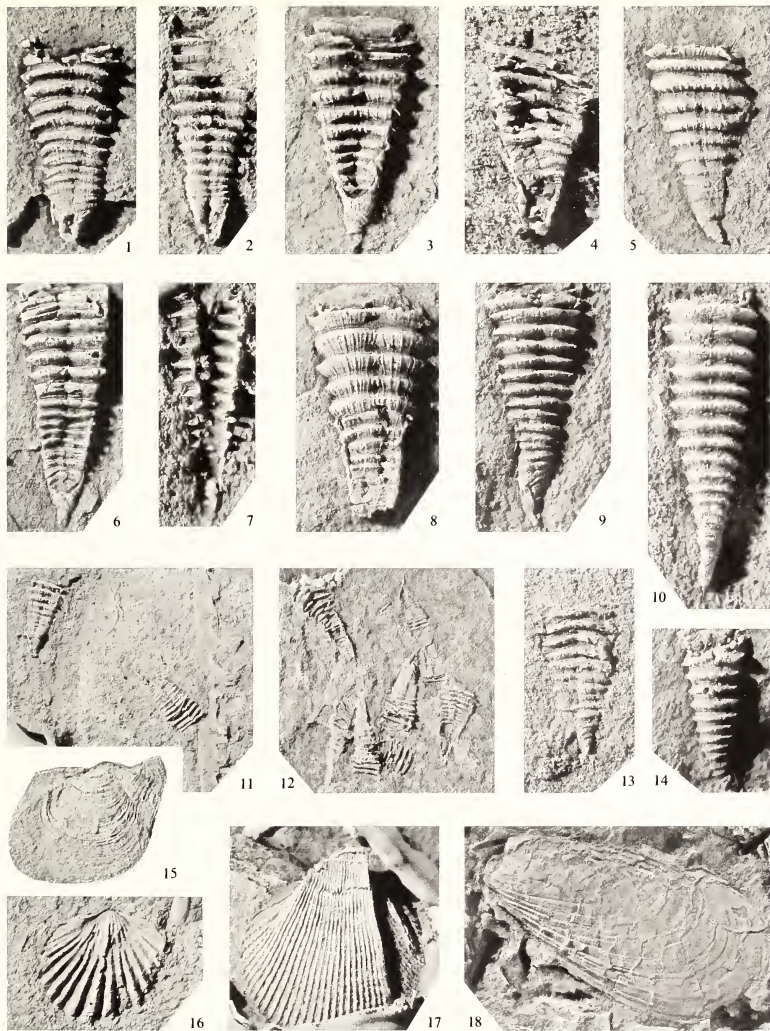
Fig. 15. *Guerichia?* sp., right valve, IGS GSM12664b, × 4.

Fig. 16. Atrypoid? gen. and sp. indet., latex cast of pedicle valve, IGS GSM104188, × 4.

Fig. 17. Lunulacardiid gen. and sp. indet., latex cast of right valve, IGS NIG592, × 4.

Fig. 18. *Mytilarca?* sp., left valve, UM K4236, × 2.

All specimens from the Limehill Beds, Llandoverly, *M. sedgwickii* Zone, Lime Hill, Pomeroy, Co. Tyrone, Ireland: IGR H 6945 7390.



Discussion. The more recently collected material allows the establishment of Portlock's manuscript name, *brevis*, with which he labelled some of his specimens although he chose not to publish it.

In all of its features this species conforms with the diagnosis of the genus *Nowakia*. Only in its growth angle does it differ from other described species of the genus, widening at almost twice (20–25°) the rate ascribed to most species (usually 10–13° in the mature portion; Fisher in Moore 1962, p. W115), and thus lacking the subcylindrical appearance in the mature portion of the shell seen in other species (Bouček 1964, pls. 1–15; Lardeaux 1969, pls. 30–36). This difference in growth angle alone is insufficient to exclude *brevis* from *Nowakia*.

The proximal end in *N. brevis* is not as globular in appearance as in some examples of *Nowakia* spp., for example some specimens of *N. acuaria* (Richter) figured by Lardeaux (1969, pl. 31, figs. 6, 7); however, the proximal end compares with specimens of *N. acuaria* figured by Bouček (1964, pl. 1, figs. 1, 6, 7; pl. 2, figs. 3, 6; pl. 3, fig. 2). There is a striking resemblance of form, sculpture, and preservation between *N. brevis* and examples of the type species *N. cancellata* (Richter), figured by Bouček (1964, especially pl. 9 and pl. 11, fig. 1), but in density of longitudinal striae *N. brevis* is closer to *N. barrandei* Bouček and Prantl (Bouček 1964, p. 75) and to *N. acuaria* (Richter) (Bouček 1964, p. 62).

The close association of *N. brevis* with *Monograptus* is noteworthy; both occur on slab IGS GSM12664, 62652 which bears the lectotype of *M. sedgwickii* (Portlock) (Pl. 84, fig. 11).

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AMMONITES POLYOPSIS DUJARDIN, 1837 AND THE CRETACEOUS AMMONITE FAMILY PLACENTICERATIDAE HYATT, 1900

by W. J. KENNEDY and C. W. WRIGHT

ABSTRACT. *Ammonites polyopsis* Dujardin, 1837 is referred to the genus *Placenticer* Meek, 1876 and shown to have priority over *Ammonites ribourianus* d'Orbigny, 1850, *Placenticer* *depressum* Hyatt, 1903, *P. grossouvrei* Hyatt, 1903 (non Semenov, 1899) (renamed *P. hyatti* Diener, 1925), *P. incisum* Hyatt, 1903, *P. schlueteri* Hyatt, 1903, and *P. crassatum* Hyatt, 1903 amongst others. This plethora of names results from early failure to recognize the strong dimorphism present in the species. Recognition of this dimorphism and the wide intraspecific variation seen in *P. polyopsis* provides a basis for a review of the Placenticeratidae and its constituent genera, of which revised diagnoses and synonymies are presented. An effect of the nomenclatorial results of the study is that the widely cited *P. syrtale* Zone should be renamed the *P. polyopsis* Zone.

THE ammonite family Placenticeratidae ranges from the upper Albian to the Maastrichtian. In all probability it was derived from the Hoplitidae via *Hengestites* Casey, 1960 and *Karamaites* Sokolov in Casey, 1965. The family is easily recognized by the multiplication of auxiliary and adventive elements in the suture line. At least twenty-four generic names have been established in the family, and a large number of specific names, yet the wide range of variability within taxa has been known for more than 150 years. Placenticeratids have a sporadic occurrence in western Europe but are sufficiently widespread and frequent in the upper Santonian and Campanian to be used as zonal indices in the standard scheme erected by de Grossouvre (1901). Although Hyatt (1903) renamed many of the European *Ammonites syrtalis* of Schlüter (1871-6) and *Placenticer* *syrtale* de de Grossouvre (1894) only two years after the *syrtale* Zone was introduced, and made it quite plain that true *P. syrtale* (a North American lower Campanian species) did not occur in Europe, the *syrtale* Zone has persisted in the literature, including the *Lexique Stratigraphique International* (e.g. Sornay 1957) and recent syntheses (e.g. Wright 1957; Basse 1960; Collignon 1960; Pessagno 1969; Séronie-Vivien 1972; Rawson *et al.* 1978; van Hinte 1979; Wiedmann 1979; Hancock and Kennedy 1981). Summesberger (1979) has used the name *Stantonoceras depressum* (Hyatt, 1903) for this European form, but has recognized dimorphism.

We describe below the material from Touraine, Aquitaine, and the Corbières in France on which de Grossouvre (1901) based the *syrtale* Zone, and show that the correct name for the species is *P. polyopsis* (Dujardin, 1837), of which *S. depressum* is a synonym. The range of intraspecific variation in *P. polyopsis* and the marked dimorphism present provides a basis for a survey of all the generic taxa proposed in the family, their diagnoses and synonymies.

SYSTEMATIC PALAEOLOGY

Location of specimens. This is indicated by the following abbreviations: BM(NH), British Museum (Natural History), London; IGS, Institute of Geological Sciences, London; MNHP, Muséum National d'Histoire Naturelle, Paris; SP, Collections of the Sorbonne, now housed in the Université de Paris VI; FSR, Faculté des Sciences, Rennes; EMP, École des Mines, Paris Collections, now housed in the Université Claude-Bernard, Lyon; FSM, Faculté des Sciences, Le Mans, which now houses the collections of the Musée de Tessé, Le Mans.

Dimensions. Dimensions are given in millimetres, in the following order: diameter (D), whorl breadth (Wb), whorl height (Wh), and breadth of umbilicus (U); c = costal; ic = intercostal. Figures in parentheses refer to dimensions as a percentage of diameter.

Suture terminology. The suture terminology of Wedekind (1916; see Kullman and Wiedmann 1970) is followed here; I = Internal lobe, U = Umbilical lobe, L = Lateral lobe, E = External lobe.

Family PLACENTICERATIDAE Hyatt, 1900

Genus *Placenticer* Meek, 1876

Placenticer *polyopsis* (Dujardin, 1837)

Plates 86–88; text-figs. 1–4

- 1837 *Ammonites polyopsis* Dujardin, p. 232, pl. 17, fig. 12.
 1850 *Ammonites polyopsis* Dujardin; d'Orbigny, p. 212.
 1850 *Ammonites Ribourianus* d'Orbigny, p. 213.
 1872 *Ammonites syrtalis* Morton; Schlüter, p. 46, pl. 14, figs. 1–10; pl. 15, fig. 5, *non* figs. 1, 2 (= copy of Morton 1834), 3–4 (= *Proplacenticer pseudorbignyanus* (Hyatt, 1903)).
non 1872 *Ammonites polyopsis* Duj. (?); Fritsch, p. 35, pl. 6, fig. 3.
 1883 *Ammonites Ribourianus* d'Orbigny; Arnaud, pl. 3.
non 1893 *Ammonites polyopsis* Duj.; Fritsch, p. 76, text-fig. 56.
 1894 *Placenticer* *syrtale* Morton; de Grossouvre (*non* Morton), p. 128 (*pars*), pl. 5, fig. 3; pl. 6, figs. 1, 2; pl. 7, fig. 1; pl. 8, fig. 1 (including var. *quadratum*).
non 1895 *Placenticer* *polyopsis* Dujardin; Jahn, p. 130.
 1903 *Placenticer* *depressum* Hyatt, p. 237.
 1903 *Placenticer* *grossouvrei* Hyatt, p. 237.
 1903 *Placenticer* *incisum* Hyatt, p. 238.
 1903 *Placenticer* *schlüteri* Hyatt, p. 239.
 1903 *Placenticer* *polyopsis* (Dujardin); Hyatt, p. 240.
 1903 *Placenticer* *crassatum* Hyatt, p. 241.
 1916 *Placenticer* *syrtale* Mort. var. *guadaloupe* F. Roemer; Stolley, p. 93, pl. 5, fig. 4.
 1925 *Placenticer* *crassatum* Hyatt; Diener, p. 185.
 1925 *Placenticer* *depressum* Hyatt; Diener, p. 185.
 1925 *Placenticer* *Hyatti* Diener, p. 185.
 1925 *Placenticer* *incisum* Hyatt; Diener, p. 185.
 1925 *Placenticer* *polyopsis* Dujardin; Diener, p. 188.
 1925 *Placenticer* *Schlüteri* Hyatt; Diener, p. 189.
 1931 *Placenticer* *syrtale* Mort. var. *guadaloupe* F. Röm.; Riedel, p. 695.
 ?1931 *Placenticer* *syrtale* Mort. cf. var. *milleri* V. Hauer; Riedel, p. 696.
 ?1931 *Placenticer* *syrtale* Mort. var. *costata* Riedel, p. 696, pl. 79, fig. 2.
 1937 *Placenticer* cf. *guadaloupe* F. Roem.; Riedel, p. 217, pl. 16, fig. 3.
 ?1937 *Placenticer* *radiatum* (J. Böhm in sched.); Riedel, p. 219, pl. 16, figs. 1, 2.
 1963 *Placenticer* cf. *hyatti* Diener; Fabre-Taxy, p. 108, pl. 3, fig. 3.
 ?1963 *Placenticer* *orbignyanus* Geinitz sp.; Fabre-Taxy, p. 109.
 1963 *Stantonoceras* *guadaloupe* Roemer sp.; Fabre-Taxy, p. 109, pl. 3, figs. 5–7.
 1963 *Stantonoceras* cf. *ribouri* d'Orbigny; Fabre-Taxy, p. 110, pl. 3, figs. 8, 9.
 1963 *Stantonoceras* *sancarlosense* Hyatt sp. var. *collignoni* nov. var.; Fabre-Taxy, p. 111, pl. 3, figs. 12, 13.
 ?1963 *Stantonoceras* sp.; Fabre-Taxy, p. 111.
 1978 *Stantonoceras* *depressum* (Hyatt); Wiedmann, p. 667, pl. 1, figs. 1, 2; text-figs. 2B, 3A.
 1979 *Stantonoceras* *depressum* Hyatt; Summesberger, p. 145, pl. 10, figs. 42, 43; pl. 11, figs. 44–47; pl. 12, figs. 48–52; text-figs. 31–37.

Types. Dujardin based this species on two specimens (1837, pl. 17, fig. 12a and b–c; see text-fig. 1). The original of his fig. 12a, a juvenile macroconch, is here designated lectotype. Both specimens are said to be from the 'Craie Tufau', and no locality, other than Touraine, is given. They have not been traced.

Material. From St.-Patern-Racan, variously labelled 'route' or 'niveau à *Spondylus truncatus*'; FSR, three specimens (plus one unlabelled that is probably from this locality); MNHP B16692; FSM, one unregistered

specimen (*ex* Guiller Coll.). MNHP B16802 from the Craie de Villedieu of Loir-et-Cher. MNHP B16802 from Couture, Villedieu-le-Château. Several specimens (Gale Coll.) from Bed 22a (Jarvis *et al.* 1982) of the Craie de Villedieu at La Ribochère, Loir-et-Cher. MNHP unregistered from near Villandry, Indre-et-Loire. MNHP unregistered from Savonnières (Indre-et-Loire). BM(NH) C26681 and an unregistered specimen in the EMP collections (*ex* Deshayes Coll.), both from Tours. EMP unregistered (*ex* Thomas Collection) from Langeais, Indre-et-Loire.

There are numerous specimens from Aquitaine. The Arnaud Collection, now in the Sorbonne Collections housed in the Université de Paris VI, includes the best localized specimens from Arnaud's assize M² at Miremont, Ribérac, Périgueux, Beaulieu (Siolac, souterrain de Beaulieu); from M¹⁻² at Angoumac, Cognac; from M² at Champagnac-de-Belair, St. Léon-sur-Vézère, Versannes, Epagnac, Miremont, Puygaty, and Rognac; one specimen is precisely located as from couche 22, route d'Agonac, Périgueux. From N¹⁻², a specimen of *P. cf. polyopsis* from St. Caprais; from N² at Arcivaux, Saintes, a *P. cf. polyopsis*. All but one of the specimens figured by de Grossouvre (1894) have not been traced (they are probably in the Université de Paris VI but are not available; a set of casts is in the collections at Rennes and those of the École des Mines, now at Lyons); they are from M² at Beaulieu, and La Valette. A specimen in the EMP collections (*ex* Boucheron Collection) is also from the last locality. A further specimen in the Collections of the Musée de Gaillac is from Charmant.

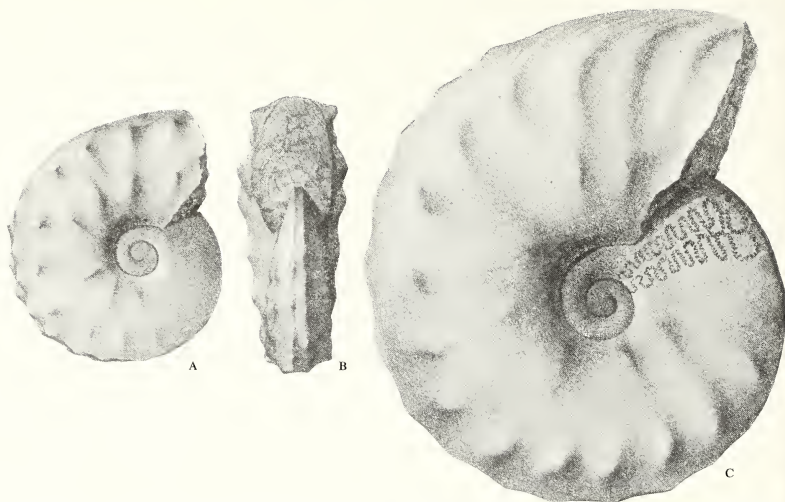
There are numerous specimens from the Corbières (Aude), variously labelled Sougraines, environs de Rennes-les-Bains, Chemin de Crouettes, etc., in the MNHP, SP, EMP, FSL, and BM(NH) collections. Stratigraphic data are usually poor, but de Grossouvre (1901, p. 795) notes that it is rare in the lower part of the Santonian but common in the upper part.

Dimensions		D	Wb	Wh	Wb:Wh	U
Microconchs:						
MNHP B16692	c	72.0 (100)	28.7 (39.9)	30.7 (42.6)	0.94	19.6 (27.2)
	ic		23.4 (32.5)	30.7 (42.6)	0.76	
FSR L803		79.7 (100)	— (—)	39.8 (49.9)	—	16.5 (20.7)
MNHP 'Villandry'	c	109.5 (100)	— (—)	46.3 (42.3)	—	26.2 (23.9)
	ic	133.0 (100)	41.4 (31.1)	55.4 (41.7)	0.75	31.5 (23.7)
MNHP unreg. at	c	109.0 (100)	41.0 (37.6)	50.0 (45.9)	0.82	23.5 (21.6)
	ic	109.0 (100)	34.0 (31.2)	47.0 (43.1)	0.72	
Macroconchs:						
MNHP 'Savonnières'		106.5 (100)	— (—)	55.0 (51.6)	—	20.5 (19.2)
MNHP 16802		141.0 (100)	— (—)	64.0 (45.4)	—	30.0 (21.3)

Description. The species is strongly dimorphic, as demonstrated by Summesberger (1979).

Microconchs. The inner whorls up to a diameter of 30–40 mm are compressed, involute, with a small crater-shaped umbilicus (around 15% of the diameter) (Pl. 87, fig. 4). The umbilical wall is flattened and slopes outwards; the umbilical shoulder is abruptly rounded. The whorl section is compressed (whorl breadth to height ratio 0.6 or less), with the greatest breadth close to the umbilical shoulder, the inner flanks rounded, the outer flanks converging to a narrow tabulate venter with sharp ventrolateral shoulders. There are feeble comma-shaped umbilical bullae (six per half whorl in MNHP B16691) which give rise to low, broad prorsiradiate ribs that flex back and are feebly concave, that is falcoid, on the outer flank, and appear to terminate in feeble ventral clavi (the specimens are defective on this point). From around 40 mm the whorls change from compressed with a narrow venter to trapezoidal with a broad, flattened venter and eventually become depressed on the adult body chamber with the greatest breadth at strong umbilicolateral bullae and below mid-flank intercostally. The feeble bullae of the inner whorls strengthen markedly, and migrate out from the umbilical shoulder to first an inner (Pl. 86, fig. 2), and ultimately a mid-flank position (Pl. 87, fig. 6). A low broad rib connects them to the umbilical seam of a large, moderately deep umbilicus, the wall of which merges imperceptibly with the flank. These tubercles are rounded to bullate, strong on the phragmocone and early body chamber of adults, but decline towards the adult aperture to weak, sharp bullae only (Pl. 85, fig. 2).

The umbilicolateral tubercles give rise to one or a pair of low, broad, straight, prorsiradiate ribs and there are also occasional short intercalated ribs to give a total of nine per half whorl. All ribs bear rounded-clavate inner ventrolateral tubercles that strengthen progressively around the outer whorl. Corresponding to each of these is a



TEXT-FIG. 1. *Ammonites polyopsis* Dujardin, 1837 (pl. 17, figs. 12a-c). Copy of Dujardin's original figures. A, B, paralectotype. C, lectotype.

sharp elongate ventrolateral clavi. This initially sits on the sharp ventrolateral shoulder of a rather narrow venter but, as size increases and the venter broadens, the clavi become progressively weaker and is eventually reduced to the merest swelling on a blunt angulation between a broad venter and broadly rounded ventrolateral shoulder. The clavi and ribs on opposite flanks vary from slightly offset to alternate in position. The venter is crossed by broadly convex growth lines and striae. The largest observed microconch (Pl. 85, figs. 1-3) has an estimated diameter of 120 mm with just over half a whorl of body chamber, the coiling becoming progressively more evolute towards the aperture.

Macroconchs. The ornament and shell form of nuclei is identical to that of the microconchs described above. The compressed, relatively feebly ornamented or smooth stage persists, however, to a diameter of 60-70 mm (Pl. 86, fig. 4); thereafter an ornament of falcoid ribs with feeble inner and stronger outer ventrolateral clavi is succeeded by an adult whorl which remains compressed but develops initially weak and bullate but subsequently strong and conical umbilicolateral tubercles which migrate to first a mid- and then an outer-flank position. These tubercles are linked to the umbilical shoulder by a low, weak rib, and give rise to a pair of low, broad, straight ribs, each of which bears a clavate inner ventrolateral tubercle. These are initially set at an angle to the line of the venter, but rotate to parallel the venter as size increases. These tubercles are invariably weaker than those of microconchs at the same diameter. Outer ventrolateral clavi are borne on the ventrolateral shoulder, generally offset from or alternating with those on the opposite side of the narrow venter. They persist to the largest diameter seen, a phragmocone 150 mm in diameter (text-fig. 2).

The suture line (text-fig. 3) follows the sagging course typical of the genus. Development of adventive and auxiliary elements gives an adult suture with eight bifid saddles in the external part.

Discussion. This species is surrounded by nomenclatorial confusion because most authors failed to recognize that individuals of the same size with markedly different ornament were dimorphs. The name *Ammonites polyopsis* was validly introduced by Dujardin in 1837, and accompanied by excellent illustrations, reproduced here as text-fig. 1.

In his description (1837, p. 232), Dujardin comments: 'Cette ammonite varie tellement, que des échantillons isolés pourraient être pris pour des espèces distinctes, si l'on n'observait quelquefois toutes les variations possibles sur les différents points d'un même échantillon.'

The lectotype (Dujardin 1837, pl. 17, fig. 12a; see text-fig. 1c) is a juvenile macroconch, and the paralectotype (Dujardin 1837, pl. 17, fig. 12b-c; see text-fig. 1A, B) is a microconch. D'Orbigny listed *A. polyopsis* in the *Prodrome* (1850, p. 212, no. 15), and indicated that there were specimens in his collection. The catalogue records two specimens under no. 7180, from Tours (Indre-et-Loire). One of these specimens survives, and is a fragment of a mature microconch. D'Orbigny also introduced the name *A. semiornatus* in the *Prodrome* (1850, p. 212). The remarks are characteristically brief: '*13. *semiornatus*, d'Orb., 1847. Espèce tres-aplatie; à tours embrassants, lisses, tronqués sur la carène, et ornés de chaque côté de cette partie de tubercles obliques. Tours, route de Paris.' This is a perfectly valid indication and two specimens survive in d'Orbigny's collection, under no. 7179. Sornay (1955) has refigured the material, referring it to *Diplacmoceras* (*recte* *Diplacmoceras*) and designating the complete specimen lectotype. Its horizon is unknown, but probably Santonian; a specimen from the Craie de Villedieu of St. Frimbault, Sarthe (MNHP de Vibraye Collection, 1896, 27) in a preservation identical to that of *Protexanites bourgeoisi* (d'Orbigny, 1850) from this locality is of upper Coniacian date. It differs from *Placenticeras polyopsis* in lacking umbilical tubercles at any stage, and in having low, rursiradiate concave ribs on the outer flank of the early stages that migrate outwards and turn into rounded or bullate inner ventrolateral tubercles that are associated with twice their number of ventral clavi. On the lectotype these rotate progressively around the body chamber to lie parallel with the venter.

A second name introduced by d'Orbigny in 1850 (p. 213) was *A. ribourianus*: '*49. *Ribourianus*, d'Orb., 1847. Espèce voisine de l'*A. polyopsis*, mais avec le dos carré, et deux rangées latérales de tubercles aigus. France, Villedieu (Loir-et-Cher), M. Bourgeois.' The asterisk indicates that d'Orbigny had specimens in his collection, but none is listed in the catalogue. From the description it clearly represents the microconch of *P. polyopsis*, body chambers of which indeed have a square back and two rows of pointed lateral tubercles.

Schlüter (1872, p. 46) treated *A. polyopsis* as a junior synonym of *A. syrtalis* Morton, 1834 (p. 40, pl. 16, fig. 4), a view followed by de Grossouvre (1894, p. 128). Both these authors recognized the wide variation in morphology and ontogeny shown by the species, and also placed *A. geinitzii* d'Orbigny, 1850 (p. 213, = *A. vibrayanus* Geinitz (*non* d'Orbigny), 1843, p. 8, pl. 1, fig. 8), *A. guadalupae* Roemer, 1852 (p. 32, pl. 2, fig. 1), and *A. milleri* Hauer, 1866 (p. 5, pl. 2, figs. 1, 2) in synonymy.

A. syrtalis Morton, 1834, is a lower Campanian species and was revised by Hyatt (1903), Reeside (1927), and Young (1963) while Wolleben (1967) has provided a valuable analysis of populations of this species. Even Hyatt (1903, p. 196) realized the wide variation of the species: 'There is no real line between *P. guadalupae*, *sancarlosense* and *planum*, nor between *newberryi* and *guadalupae*, nor between *sancarlosense*, *syrtale*, *intercalare* and *placenta*, nor between *intercalare*, *stantoni*, *pseudoplacenta* and *whitfieldi*.' Wolleben (1967) placed all these species in synonymy, as well as *Stantonoceras pseudocostatum* Johnson, 1903 and *P. rotundatum* Johnson, 1903. He recognized, however, a series of chronological subspecies: *P. syrtale syrtale* (oldest), in which specimens of '*P. syrtale*' of previous authors are abundant, *P. syrtale adkinsi* Wolleben, 1967, in which specimens of '*P. pseudosyrtales*' of previous authors are abundant, and *P. syrtale rooneyi* Wolleben, 1967, in which specimens of '*P. newberryi*' of previous authors are abundant. Nomenclatorial problems of this treatment aside, it was unfortunate that Wolleben failed to recognize that this species shows the same type of dimorphism as *P. polyopsis*, with robust '*Stantonoceras*' microconchs and '*Placenticeras*' macroconchs.

P. syrtale is superficially similar to *P. polyopsis*, but Hyatt (1903) recognized them as separate, noting that juveniles of the American species lack ribs on the inner whorls and that umbilical bullae remain on the umbilical shoulder, not showing the outwards migration of the French specimens. The sutures are also different, *P. polyopsis* having eight lobes in the external suture and *P. syrtale* ten or eleven.



TEXT-FIG. 2. Immature macroconch of *Placentiaceras polyopsis* (Dujardin, 1837), MNHP B16802, from 'Loir-et-Cher', $\times 1$.

EXPLANATION OF PLATE 85

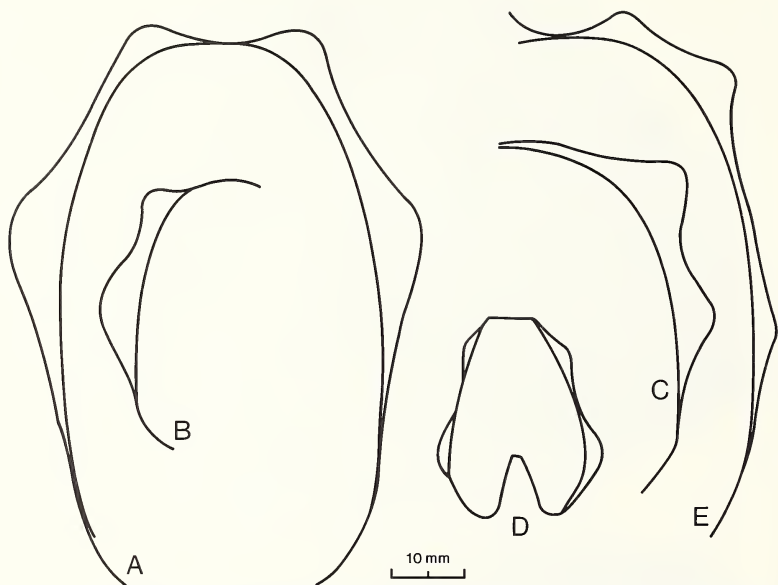
Figs. 1-3. *Placentiaceras polyopsis* (Dujardin, 1837). Slender microconch from the Santonian Craie de Villedieu of Touraine (MNHP unregistered, ex de Grossouvre Collection). $\times 1$.



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TEXT-FIG. 3. External suture of *Placenticerias polyopsis* (Dujardin, 1837), based on an unregistered specimen in the Sorbonne Collections (ex Toucas Collection), from near Sougraines, Corbières, Aude.



TEXT-FIG. 4. Whorl sections of *Placenticerias polyopsis* (Dujardin, 1837). A, slender microconch (see Pl. 86, figs. 1-3 for details). B, C, microconch from Couture, MNHP B16805; B is at the beginning of the body chamber, C at the end. D, phragmocone of an immature microconch from near Villandry, MNHP collections. E, phragmocone of macroconch shown in text-fig. 2.

EXPLANATION OF PLATE 86

Figs. 1-5. *Placenticerias polyopsis* (Dujardin, 1837). 1-3, MNHP B16692, immature microconch from the Santonian Craie de Villedieu of St-Paterne-Racan, Indre-et-Loire. 4, 5, MNHP B17228, immature macroconch from the Santonian of Paulin, Dordogne. All $\times 1$.



Hyatt (1903) renamed most of Schlüter's (1872) and de Grossouvre's (1894) *A. syrtalis* and *P. syrtale*. *P. depressum* Hyatt, 1903 (p. 237) (= *A. syrtalis* Schlüter (non Morton), 1872, p. 46 (*pars*), pl. 14, figs. 9, 10 only; *P. syrtale* var. *Guadaloupae* de Grossouvre (non Roemer) 1894, p. 128, pl. 6, fig. 2 only; pl. 7, fig. 1, lectotype here designated, the original of de Grossouvre 1894, pl. 6, fig. 2) is a microconch *P. polyopsis*. *P. hyatti* Diener, 1925 *nom. nov. pro P. grossouvrei* Hyatt, 1903 (p. 237) (non Semenov, 1899) = '*Placenticeras syrtale* de Grossouvre (*pars*), p. 128, pl. 5, fig. 32, p. 16, fig. 1 (no others)' was cited erroneously in Hyatt's posthumous work, 'pl. 5, fig. 32, p. 16, fig. 1' not existing in de Grossouvre's work. From the subsequent account, however, it is apparent that the intended citation was 'pl. 5, fig. 3, pl. 6, fig. 1'. The latter is here designated lectotype of the species; it is an adult macroconch. The paralectotype is a juvenile 55 mm in diameter that already has ribs and tubercles at the smallest diameter visible, indicating it to be a juvenile microconch.

P. incisum Hyatt, 1903 (p. 238) (= *P. syrtale* de Grossouvre, 1894, p. 128 (*pars*), pl. 8, fig. 1 only) is based on a macroconch from assize M² of Arnaud at La Valette (Charente) (Rejaudry Collection). It has not been traced (but there are casts in the FSR and EMP collections) and a fine unlocalized specimen in the MNHP collections, illustrated here as Pl. 85, figs. 1–3, serves as a basis for discussion. The dimensions are given above. Ornament consists of umbilicolateral tubercles, of which there are seven on the outer whorl. These are weak and markedly bullate at the smallest diameter visible, but strengthen markedly and migrate outwards around the last whorl and are connected to the umbilical seam by a low rib. Very weak pairs of ribs link to strong inner ventrolateral clavi, whilst additional clavi are intercalated to give a total of approximately twenty per whorl. Those on opposing flanks are slightly offset in ventral view, rising high above the narrow venter. At the smallest diameter visible a semicontinuous ridge or angulation marks the junction of venter and ventrolateral shoulder, but this declines on the body chamber where the venter is smooth and concave between persistent ventral clavi. This early decline of outer ventrolateral clavi, and the angulation marking their site which disappears on the body chamber, are features of microconch *P. polyopsis*, but these are generally depressed and quadrate. At the same diameter, similarly compressed macroconchs are still septate and retain discrete outer and inner ventrolateral clavi. The species is interpreted as an unusually compressed microconch of *P. polyopsis*.

P. schluteri Hyatt, 1903 (p. 239) (= *A. syrtalis* Schlüter (non Morton), 1872, p. 46 (*pars*), pl. 14, figs. 1, 2) was separated by Hyatt on the basis of details of ornament and ontogenetic changes in tuberculation. The specimen shows the same outward migration of umbilicolateral tubercles as *P. polyopsis* but lacks ribs on the inner flank; it is a clear synonym, and probably a microconch. *P. crassatum* Hyatt, 1903 (p. 241) (= *A. syrtalis* Schlüter (non Morton), 1872, p. 46 (*pars*), pl. 14, figs. 4–7, fig. 3?) was differentiated from *P. schluteri* by Hyatt because it was more compressed and did not show an outward migration of the umbilicolateral tubercles which disappear and are replaced by low ribs. This is probably no more than a variant of *P. polyopsis*.

P. pseudorbignyanum Hyatt, 1903 (p. 242) (= *A. syrtalis* Schlüter (non Morton), 1872, p. 46 (*pars*), pl. 15, figs. 3–5 only) is a member of the Coniacian *P. orbignyanum* (Geinitz, 1850) group which lacks the strong tubercles of the later *P. syrtale*. Other members are *P. fritschii* de Grossouvre, 1894 (p. 124, pl. 5, figs. 1, 2; text-fig. 52) (the type species of *Proplacenticeras* Spath, 1926), *P. memoriaschloenbachi* (Laube and Bruder, 1887) (p. 221, pl. 23, fig. 1), *P. kaffrarium* (Etheridge, 1904) (p. 89, pl. 3, fig. 16), *P. umkwelanensis* (Etheridge, 1904) (p. 89, pl. 3, figs. 17–20), and *P. subkaffrarium* (Spath, 1921)

EXPLANATION OF PLATE 87

Figs. 1–6. *Placenticeras polyopsis* (Dujardin, 1837). 1, 2, SP unregistered, juvenile microconch from the Souterrain de Beaulieu on the line from Ribérac to Périgueux, Dordogne; figured by de Grossouvre (1894, pl. 5, fig. 3). 3, 4, MNHP B16691, incomplete microconch showing smooth inner whorls, from the Santonian Craie de Villedieu of Monnat, near Villandry, Indre-et-Loire. 5, 6, MNHP unregistered, incomplete microconch from the Santonian Craie de Villedieu, 2 km west of Villandry, Indre-et-Loire. All $\times 1$.



KENNEDY and WRIGHT, *Placenticerus*

(p. 247, pl. 21, fig. 2). These show a wide range of intraspecific variation and dimorphism comparable in some respects to that seen in *P. polyopsis*, as will be discussed in a forthcoming publication.

P. syrtale costata Reidel, 1931 (p. 696, pl. 79, fig. 2) from the Santonian of Ziegeli near Recklinghausen in the Münster Basin is regarded as no more than a variant of the present form, as is *P. radiatum* Riedel, 1937 (p. 219, pl. 16, figs. 1, 2) from the Santonian of Heudeber-Danstedt in the Harz Foreland. However, more and better material of both forms might in future indicate consistent differences justifying subspecific separation.

P. paraplanum Wiedmann, 1978 (p. 666, pl. 1, figs. 3, 4, text-fig. 2A; see also Summesberger 1979, p. 152, pl. 13, figs. 53–57, text-figs. 38, 39) which occurs with *P. polyopsis* in the upper Santonian Gosau Beds of Gosau, Austria. It appears to be separate from *P. polyopsis* on the basis of strongly convex flexuous ribs and bullae that remain closer to the umbilical shoulder. Wiedmann compared it to *P. planum* Hyatt, 1903, which Wolleben (1967) considered no more than a variant of *P. syrtale*, and it may lie in an analogous position in the spectrum of variation of *P. polyopsis*. One of the specimens referred to the species by Summesberger (1979, pl. 13, figs. 55, 56) shows an outward migration of the umbilicolateral bulla and an early decline of the outer ventrolateral clavi.

P. maherndti Summesberger, 1979 (p. 155, pl. 14, figs. 58–61; pl. 15, figs. 62–66, text-figs. 40–47) is a much better characterized species in which Summesberger was also able to recognize dimorphism. It occurs with *P. polyopsis* in the upper Santonian Gosau Beds of Gosau, Austria. Inner whorls bear falcoid ribs, the macroconch develops weak bullae, and body chambers of both forms bear dense flexuous ribs. Distinct as this appears, the material is no more different from the *P. polyopsis* described here than the extremes of *P. syrtale* discussed by Wolleben (1967) are from each other.

Occurrence. The species is confined to the Santonian. In Touraine it occurs widely in the Craie de Villedieu, well-localized specimens coming from de Grossouvre's (1901) Zone E, the niveau à *Spondylus truncatus* of previous authors. Jarvis *et al.* (1982) have shown that the species occurs in the remanié lag at the top of a hardground (their bed 22a) at Villedieu; the preservation of other specimens suggests a similar occurrence. The only associated fauna of stratigraphic significance is *Baculites incurvatus* Dujardin, 1837. In Aquitaine the species is widespread, as indicated under the list of specimens studied, and Arnaud (1877) cited it from many other localities (see also Séronie-Vivien 1972). The stratigraphic range spans all of Arnaud's divisions of the Santonian (M¹, M², N¹, N²), and this is confirmed by records in Toucas (1883), de Grossouvre (1894, 1901), and Séronie-Vivien (1972). The last author recorded it from only 5 m above the base of the Santonian in a temporary trench at L'Amblardie, Montmoreau (p. 78), and low in the Santonian at Castelfadèze and Mater (pp. 89, 144). Indeed, most of Arnaud's specimens are from his divisions M¹ and M²—that is to say, the lower Santonian *Texanites texanus* Zone of de Grossouvre.

In the Corbières the reliable records are still those of de Grossouvre (1894, 1901), who recorded it as rare in the lower part of the sequence (his *texanus* Zone) but common above (the 'banc à *Lima marticensis*' and the 'marnes intercalées entre les deux principaux bancs de rudistes'). This is what Billotte *et al.* (1971) referred to as the 'Série de la Montagne des Cormes'. The species occurs at many localities in the Beausset Basin (Var) (de Grossouvre 1894, 1901; Fabre-Taxy 1963). Fabre-Taxy assumed all the occurrences to be in the upper Santonian.

In Austria the species is abundant in the Gosau and Piesting areas (Wiedmann 1978; Summesberger 1979, 1980). The Gosau records are in the 20 m thick 'sandkalkband' at the top of the Santonian. This species occurs widely in the Germanies, and Mr. C. J. Wood has kindly analysed the best-documented occurrences. At Deitermann's brick-pit at Rapen, near Recklinghausen, the Recklinghausen Marl yielded *P. polyopsis* associated with *Boehmoceras krekeleri* (Wegner, 1905) and *B. loescheri* (Riedel, 1931) and other species. These suggest the upper Santonian on the basis of Summesberger's records and the occurrence of *Boehmoceras* in Arnaud's Assizes M² and N² in Aquitaine. The Recklinghausen occurrences are associated with *Marsupites*, indicating the *M. testudinarius* Zone of the north-west European White Chalk facies. Böhm (1915) recorded *P. schlucteri* Hyatt, 1903 (e.g. *P. polyopsis*) associated with *B. krekeleri* and other ammonites in the *M. testudinarius* Zone at Ahaus. Riedel (1937) recorded what are here interpreted as *P. polyopsis* from the Salzberg Marl of the Quedlinburg-Salzberg region; the associated inoceramid evidence indicates the high *Micraster coranguinum* Zone of the White Chalk facies. He recorded from Heudeber-Danstedt what he believed to be different species, *P. radiatum* and *P. intercalare*, herein regarded as *P. polyopsis*, associated with a fauna indicating a higher horizon than that at Salzberg.

The more general records of Wiedmann (1979) appear to be based chiefly on Schlüter's early records; they

suggest *P. polyopsis* is confined to the upper part of the Santonian; indeed, Wiedmann uses the term *syrtale* Zone in de Grossouvre's sense.

These data suggest that *P. polyopsis* ranges from just above the base of the Santonian in Aquitaine to the highest of Arnaud's divisions (from M¹ to N²). Most of the surviving specimens are labelled M¹, but there are so few that this may not reflect real abundance. In the Corbières the species occurs both low and high in the Santonian but is commonest above. The same appears to be true in Provence and in Germany and Austria. The Touraine records are stratigraphically isolated and cannot be referred to either upper or lower Santonian with any confidence at this time. The absence of diagnostic elements of the high Santonian crinoid zones of the White Chalk facies (Jarvis *et al.* 1982) suggest it is lower Santonian, however, as that term is used in the chalk sequences.

Dr. W. A. Cobban (pers. comm., 1982) tells us that he believes fragments of *Placenticer* from the Tombigbee Sand Member of the Eutaw Formation of Alabama can be referred to the present species; the unit is assigned to the Santonian on other evidence.

DISCUSSION

Stratigraphic consequences. The upper Santonian *P. syrtale* Zone of de Grossouvre and authors should be renamed the *P. polyopsis* Zone. The index species, however, has a range that extends into the lower Santonian.

Systematic consequences. The recognition of wide intraspecific variation and dimorphism in *P. polyopsis* leads to a critical review of the systematics of the Placenticeratidae.

The family appears to have evolved rapidly in the upper Albian from *Metaclavites* Casey, 1965 (Hoplitinae) by increase in whorl height and associated development of extra elements in the suture. Almost all members of the family up to the Maastrichtian show at some stage of ontogeny the alternating ventrolateral clavi that characterize their hoplitine ancestors.

In the upper Albian there are three genera whose interrelationships are not yet clear. *Hengestites* Casey, 1960, known only from England, has a juvenile stage with feeble flexuous ribs ending in fine ventrolateral clavi. The shell then becomes smooth with sharp-edged, sulcate, later tabulate, venter; the suture is not far removed from that of Hoplitinae but shows major subdivision of saddle E/L. *Hypenogoceras* Spath, 1922, known from Spain, Madagascar, Zululand, southern India, and perhaps Japan, has low falcoid ribs and ventrolateral clavi to a late stage, together with a suture characterized by many subequal pincer-like saddles. The third genus, for which *Karamaites* Sokolov in Casey (1965, p. 461) is the earliest of seven names which we regard as synonymous, ranges from upper Albian to Cenomanian and is known from France, Crimea, and Central Asia. It has flat sides on the early whorls which become convex later, and ventrolateral tubercles which persist to a variable extent. The suture is also variable but the 4th lateral lobe is generally smaller than the 5th.

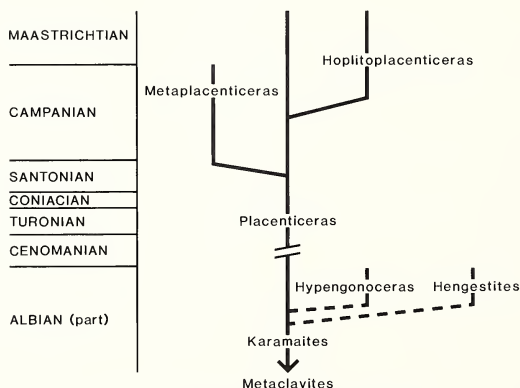
Karamaites begins the mainstream of the family which continues with slow elaboration of ornament and suture until the Maastrichtian. Marked dimorphism can be demonstrated whenever large collections of upper Cretaceous specimens are examined. We have insufficient Albian material to pronounce on dimorphism, but in the upper Cenomanian *Proplacenticer* from Texas it is obviously present, the macro- and microconchs differing in size, but little else. By the upper Turonian the Madagascan faunas show an association of large forms that are said to be smooth when adult, except for minute umbilical tubercles (*Proplacenticer* *memoriaschloenbachi* var. *ambiloensis* Collignon, 1965a, p. 14, pl. 381, fig. 1646; pl. 382, figs. 1647–8), and smaller forms with stronger umbilical bullae and weaker clavate mid-lateral to inner ventrolateral and outer ventrolateral tubercles (*Parastantonoceras* *murphyi* Collignon, 1965a, p. 17, pl. 382, fig. 1649); these we take to be macro- and microconchs respectively. The same type of dimorphism may also be present in the so-called 'Middle' Turonian of Madagascar (see Collignon 1965a, pl. 383), with '*Parastantonoceras*' *besairiei* (Collignon, 1936) as microconch, and in the Coniacian with *Proplacenticer* *fritschii* *eboroensis* Collignon, 1965b (p. 38, pl. 430, figs. 1780–1781) as macroconch and *P. kaffrarium* (Etheridge, 1904) as microconch (the nomenclature of Coniacian '*Proplacenticer*' is as confused as that of the Santonian species of *Placenticer* and is not entered into here).

The dimorphism shown by the European *Placenticer* *polyopsis* is described above. Suture line apart, macroconch *Placenticer* and '*Proplacenticer*' are very similar, differing only in the degree

of retention of strong ornament and outward migration of umbilical bullae and mid-lateral clavi. The microconchs become more evolute and are sometimes quadrate in whorl section, with persistent ornament. The same is true of the Campanian *Placenticerus syrtale* group, as documented, but not recognized, by Wolleben (1967).

Two stocks separated from *Placenticerus* in the Santonian that in our view clearly deserve generic separation. *Metaplacenticerus* Spath, 1926, is characterized by dense strong flexuous ribbing and no tubercles. We have not seen enough material to recognize dimorphism. *Hoplitoplacenticerus* Paulcke, 1906, is relatively evolute with a more or less rectangular whorl section and strong ribs and tubercles and lacks a smooth stage. Preliminary observations on material from Zululand (South Africa) indicate dimorphism.

Given the wide range of variation of ornament and progressive increase in numbers of sutural elements, it is difficult to decide on any split in generic classification of the mainstream forms. It would be attractive to refer the whole of the mainstream of the family to one genus, *Placenticerus*, with *Karamaites*, *Proplacenticerus*, and *Placenticerus sensu stricto* as successive subgenera for those who can find significance in minor sutural differences. It is in our view practicable in the present state of knowledge to distinguish *Karamaites*, generically or subgenerically, for early forms in which definite dimorphism is not yet demonstrated. *Proplacenticerus*, however, is tied to its type species, *Placenticerus fritschii* Grossouvre, and study of the type material shows that it is either conspecific with or very closely allied to contemporary material from Zululand (Klinger and Kennedy 1980, p. 305) that covers a morphological range almost as wide as that of Santonian *Placenticerus*. The progressive increase in the number of auxiliary elements in the suture does not, we believe, allow any sensible division; if reliance were placed on this character a distinct genus or subgenus would logically have to be based on each increase of one new auxiliary lobe in the adult suture. The outward migration in strongly ornamented forms of umbilical tubercles to a mid-lateral position and of mid-lateral tubercles to an inner ventrolateral position is equally continuous. Our conclusion is that we should for the present at least maintain *Karamaites* for mainstream forms that show no strong differentiation of dimorphs and group in *Placenticerus* those upper Cenomanian, Turonian, and later species, including the type species of *Proplacenticerus*, that have strongly differentiated microconchs. If *Karamaites* is subsequently found to have strongly differentiated microconchs, it should be reduced to a synonym of *Placenticerus*. We would thus set out the classification of the family as follows (see also text-fig. 5):



TEXT-FIG. 5. Phylogeny of the Placenticeratidae.

Family PLACENTICERATIDAE Hyatt, 1900, p. 585

(= Hypengonoceratidae Chiplonkar and Ghare, 1976, p. 2; Baghiceratinae Chiplonkar and Ghare, 1976, p. 3)

Diagnosis. Moderate-sized to large; inner whorls at least generally involute, compressed, with narrow flat or grooved venter and little or no ornament; outer whorls similar in macroconchs; microconchs of some genera become evolute and more or less inflated with strong ornament. Suture with adventive and auxiliary elements; the external saddle and first lateral lobe become very wide and develop a number of more or less equal new elements; saddles and lobes may be short and more or less rounded, or long, narrow-necked, and much frilled. Of Albian genera, while *Hypengonoceras* in some respects resembles Engonoceratidae, *Hengestites* and *Karamaites* are clearly derived from Hoplitidae.

Occurrence. Upper Albian to Maastrichtian.

Genus *Hengestites* Casey, 1960, p. 201

Type species. *Hengestites applanatus* Casey, 1960, p. 201, by original designation.

Diagnosis. Large, high-whorled, involute with angular umbilical rim and narrow venter. Early whorls have faint flexuous riblets ending in alternating ventrolateral clavi. Later shell is smooth, the venter sulcate with carinate edges, then tabulate. Suture with shallow ventral lobe, a broad bifid or asymmetrically trifid first lateral lobe, bifid and subphylloid saddles; a deep adventitious lobe divides the external saddle unequally, the ventral part being much smaller.

Occurrence. Upper Albian; England.

Genus *Hypengonoceras* Spath, 1922, p. 112

Type species. *Placenticerus warthi* Kossmat, 1895, p. 92, by original designation.

Diagnosis. With sloping flat sides and narrow flat venter; sparse low falcoid ribs end in alternating ventrolateral clavi. Suture with large pincer-like bifid folioles.

Occurrence. Upper Albian; Spain, Madagascar, Southern India, ?Japan.

Genus *Karamaites* Sokolov in Casey, 1965, p. 461

Synonyms. *Karamaites* Sokolov, 1961, p. 152 (*nom. nud.*); *Karamaiceras* Sokolov, 1967, p. 138; *Turkmenites* Ilyin, 1975, p. 154; *Kopetdagites* Ilyin, 1975, p. 157; *Mediasiceras* Ilyin, 1975, p. 159; *Beschitubites* Ilyin, 1975, p. 162.

Type species. *Placenticerus grossouvrei* Semenov, 1899, p. 97, by original designation.

Diagnosis. Sides flat at first, then inflated and convex; weak sinuous to falcoid ribs may be present on early whorls, with little ornament except for prominent alternate ventrolateral clavi which persist to body chamber. Suture with 4th lateral lobe generally smaller than 5th. So far as is known, dimorphs are not strongly differentiated.

Occurrence. Upper Albian to Cenomanian; France, Central Asia.

Genus *Placenticerus* Meek, 1876, p. 462

Synonyms. *Placentoceras* Meek, 1871, p. 429, *nom. oblit.*; *Diplacomoceras* Hyatt, 1900, p. 585; *Diplacomoceras* Hyatt, 1903, p. 242; *Stantonoceras* Johnson, 1903, p. 208; *Proplacenticerus* Spath, 1926, p. 79; *Pseudoplacenticerus* Spath, 1926, p. 79; *Anaplacenticerus* Ilyin, 1959a, p. 201; *Gissarites* Ilyin, 1959b, p. 727; *Parastantonoceras* Collignon, 1965a, p. 17; *Asiatostantonoceras* Ilyin, 1975, p. 172; *Baghicerus* Chiplonkar and Ghare, 1976, p. 3; *Mahwicerus* Chiplonkar and Ghare, 1976, p. 4; *Placentoscaphites* Chiplonkar and Ghare, 1977, p. 68; *Sancarlosia* Chiplonkar and Ghare, 1978, p. 79.

Type species. *Ammonites placenta* DeKay, 1828, p. 278, by subsequent designation by Meek, 1876, p. 462.

Diagnosis. Distinguished from *Karamaites* by progressive increase in number of elements in the suture line, by development of strongly differentiated microconchs, and by progressive outward migration of umbilical tubercles to mid-lateral and mid-lateral to inner ventrolateral positions. Extreme forms are smooth, involute discs with narrow tabulate venters on the one hand and on the other forms with evolute, square-sectioned outer whorls with strong ribs and lateral and ventrolateral tubercles.

Occurrence. Upper Cenomanian to Maastrichtian; world-wide.

Genus *Metaplacenticer* Spath, 1926, p. 79

Synonym. *Paraplacenticer* Matsumoto, 1953, p. 149.

Type species. *Placenticer pacificum* J. P. Smith, 1900, p. 187, by original designation of Spath, 1926, p. 79.

Diagnosis. Compressed and flat-sided; with rather strong falcid or falcate ribs; venter distinctly tricarinate, at least in middle growth. Line of suture follows that of ribs.

Occurrence. ?Santonian, Campanian; Japan, California.

Genus *Hoplitoplacenticer* Paulcke, 1906, p. 183 (ICZN name no. 1348)

Synonym. *Dechenoceras* Kayser, 1924, p. 175.

Type species. *Hoplitoplacenticer plasticus* Paulcke, 1906, p. 186: ICZN Opinion 554, 1959: name no. 1629.

Diagnosis. Rather evolute, whorl section compressed or trapezoidal, venter flat; with prominent variable coarse rounded or dense fine ribs, nearly straight, with inner and outer ventrolateral tubercles, of which outer may be large and clavate; ribs cross venter transversely and may have trace of siphonal tubercle.

Occurrence. Campanian–Maastrichtian; France, Germany, West Africa, Egypt, Zululand (South Africa), India, British Columbia, Texas, Wyoming, Patagonia.

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CAMBRIAN ORIGINS OF THE ODONTOPLEURID TRILOBITES

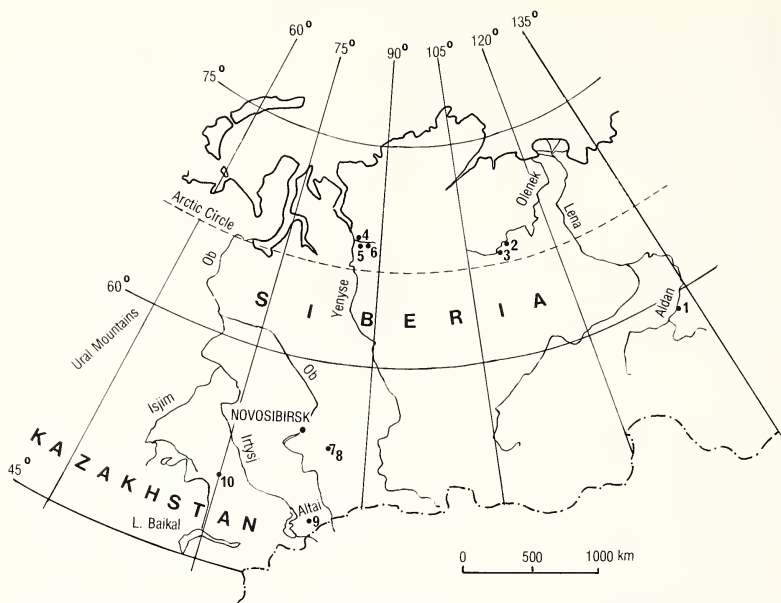
by DAVID L. BRUTON

ABSTRACT. Type and topotype material of middle and upper Cambrian odontopleuracean trilobites is described from the Soviet Union and new family and generic diagnoses are given. *Belovia*, *Acidaspidea*, and *Eoacidaspis* are assigned to the Family Eoacidaspididae, *Acidaspides* and *Acidaspidea* to the Odontopleuridae. Holaspid cranidia of *Acidaspides* resemble those of early Ordovician *Primaspis* (Odontopleurinae), pre-holaspid growth stages resemble certain Miraspidinae, and *Acidaspidea* resembles *Leonaspis*. This confirms the view of Whittington that *Primaspis* and *Leonaspis* are among the root-stocks of the Odontopleurinae. The range of the Odontopleuridae is middle Cambrian to upper Devonian making this one of the longest living trilobite families.

AMONGST the rich diversity of trilobites inhabiting marine environments in the Ordovician, Silurian, and Devonian are those which form a small family group, the Odontopleuridae. Their characteristic pustulose or thorn-like surface sculpture, lobate glabella, and spinose margins are features that allow even fragmentary material to be readily identified. The post-Cambrian life-span of the family is approximately 160 million years covering the period from the lower Ordovician (Arenig) to the upper Devonian. The origin of most Ordovician and later trilobite groups is cryptogenetic (Stubblefield 1960), but odontopleuracean ancestors are to be found among middle and upper Cambrian trilobites recorded in the last thirty years or so from Siberia, Kazakhstan, and China. Original type material is not well preserved, but in April and May 1965 I was able to examine this and additional material preserved at the Geological Institute, Moscow, and the Central Geological Museum (VSEGEI), Leningrad. Material from the Siberian Geological Institute (SNIIGGIMS), Novosibirsk, was obtained on loan and examined in Moscow. Latex moulds were taken of all specimens and a set of plaster casts made to illustrate this present work. These casts, together with actual specimens kindly presented to me by Drs. Pokrovskaya, Tchernysheva, and Lazarenko, are now housed in the Paleontologisk Museum, Oslo (hereafter abbreviated PMO).

Three publications by Professor H. B. Whittington, F.R.S. (Whittington 1956*a*, *b*; Whittington and Bohlin 1958), first drew my attention to the Odontopleuridae, and he has been a constant source of inspiration to me in my own interest in this group (Bruton 1968 and references). Whittington frequently commented on the long time range of certain genera. *Miraspis*, a genus widespread in Europe and North America, ranges from the Arenig (Whittington and Bohlin 1958) to the lower Devonian (Whittington 1956*a*) and its species exhibit so little variation that it is difficult to separate them. Evidence suggests that an animal well adapted to a particular environment may last for long periods without undergoing significant morphological change (Whittington 1962, p. 415). The nature of the environment in which odontopleurids lived is not known and while their thoracic and pygidial spines have suggested a floating or drifting habit, other spines, such as those along the antero-lateral cephalic margin, aided resting on the sea floor and thus a benthonic habit (Whittington 1956*b*; Clarkson 1969). In the following discussion it is shown that described middle and upper Cambrian trilobite faunas contain forerunners of the Odontopleuridae demonstrating that the family has one of the longest evolutionary histories among the Trilobita.

Text-fig. 1 shows the geographical distribution of odontopleuraceans described from the upper Cambrian of Kazakhstan (Lermontova 1951; Chugaeva and Apollonov 1982) and the middle and upper Cambrian of Siberia (Tchernysheva 1953, 1960*b*; Poletaeva 1956, 1960*a*, 1960*b*, 1969, 1977; Lazarenko 1960, 1968; Rozova 1963, 1964, 1968; Lazarenko and Datsenko 1967; Lazarenko and



TEXT-FIG. 1. Map of Siberia and part of Kazakhstan with type localities for: (1) *Acidaspides lermontovae*; (2) *Belovia calva*; (3) *Acidaspides borealis*; (4) *Acidaspidina plana*; (5) *Acidaspidella limita*; (6) *Eoacidaspis amplicauda*, *Belovia aliquantula*, *B. laeta*, *B. cyclica*; (7) *Eoacidaspis salairica*; (8) *Belovia salairica*, *B. radugini*; (9) *B. media*; (10) *Acidaspides precurrens*.

Nikiforov 1968; Zuravleva and Rozova 1977). Material has also been recorded from the upper Cambrian of South China (Poletaeva 1960a), although it is not well known. The first taxon to be described from the Soviet Union was the upper Cambrian *Acidaspides precurrens* Lermontova, 1951 (pp. 27–29, pl. 6, figs. 4–9; herein Pl. 88, figs. 12, 15). Later Tchernysheva (1953, pp. 81–82, pl. 6, figs. 16–17) described *A. lermontovae* (Pl. 88, fig. 7) from the late middle Cambrian. Poletaeva (1956) established two monotypic genera, *Belovia* (middle–upper Cambrian) and *Eoacidaspis* (upper Cambrian), and later (Poletaeva 1957, pp. 162–164) the new family Eoacidaspidae (Eoacidaspidae *nom. correct.* Jaanusson in Moore 1959, p. O509) was erected to embrace these genera and *Paraacidaspis* Poletaeva, 1957 *nom. nud.* (non 1960 *nom. nud.*). The Eoacidaspidae were regarded as a primitive branch of odontopleuraceans which became extinct in the upper Cambrian. *Acidaspides* was considered to be a direct ancestor of the post-Cambrian odontopleurids and was thus included in the Odontopleuridae. More recently *Acidaspidina* Lazarenko, 1960 and *Acidaspidella* Rozova, 1963 non Pokrovskaya, 1961, have been described from the upper Cambrian of Siberia.

All known material is of cranidia, associated pygidia being only doubtfully assignable to this group.

In the following account, evidence is produced to show that *Acidaspidina* (early upper Cambrian) was derived from the same root-stock that gave rise to *Eoacidaspis* (late upper Cambrian) and that these and *Belovia* (middle-early upper Cambrian) together form the Eoacidaspididae. *Acidaspidella* (upper Cambrian) and *Acidaspides* (middle Cambrian-?Tremadoc) were derived from a *Belovia*-like root-stock and gave rise to the post-Cambrian Odontopleuridae to which family they are assigned.

SYSTEMATIC PALAEONTOLOGY

Family EOACIDASPIDIDAE Poletaeva, 1957

Diagnosis. Anterior facial sutures strongly divergent in front of eyes. Latter placed far back, eye ridges prominent. Cranium with prominent anterior border, separated from glabella by distinct furrow. Glabella long (sag.), trapezoidal, occipital ring narrow, occipital furrow deep, curved forward medially. Dorsal furrows well-defined posteriorly, deflected around L2. Latter oval, S1 deepened at inner end, S2 and S3 weak to obsolete. Surface smooth to weakly granulose.

Stratigraphical range. Late middle Cambrian to Tremadoc.

Genera. *Eoacidaspis* Poletaeva, 1956; *Belovia* Poletaeva, 1956; *Acidaspidina* Lazarenko, 1960.

Discussion. Poletaeva (1957) recognized two distinct root-stocks in the late middle Cambrian and established the family Eoacidaspididae (*nom. correct.*) for *Eoacidaspis* and *Belovia*. While leaving *Acidaspides* unassigned, she recognized that this genus should be regarded as a possible ancestor of the post-Cambrian odontopleurids. In 1960 she repeated this idea (Poletaeva 1960a), and emended the family diagnosis to accommodate a third genus, *Paraacidaspis* *nom. nud.* This seems to have been overlooked by subsequent revisers (Jaanusson *in* Moore 1959; Kobayashi and Hamada 1977) including most Soviet palaeontologists who assign all Cambrian odontopleuraceans to the Eoacidaspididae. However, Maximova *in* Tchernysheva (1960a) followed Poletaeva's original suggestion regarding the Eoacidaspididae, but assigned *Acidaspides* to the Odontopleurinae (= Odontopleuridae). Study of all the material in question has led me to similar conclusions, summarized in text-fig. 2. I thus believe that *Acidaspidina* was derived from the same root-stock that gave rise to *Eoacidaspis* and that these and *Belovia* together form the Eoacidaspididae. *Acidaspidella* Rozova, 1963 and *Acidaspides* Lermontova, 1951 are assigned to the Odontopleuridae Burmeister, 1843 (see Whittington *in* Moore 1959), *Acidaspides* being a direct ancestor of the post-Cambrian Odontopleurinae. Features shared between *Acidaspidella* and *Acidaspides* include the narrow upturned anterior border, straight anterior facial suture, well-defined dorsal furrows, and long (sag.) occipital ring with median tubercle. The sinuous dorsal furrow and the prominent L2 lobe in *Acidaspidella* is a feature shown in *Acidaspidina*, suggesting that the odontopleurid line was derived from the same root-stock which gave rise to *Acidaspidina* and *Eoacidaspis* sometime in the late middle Cambrian.

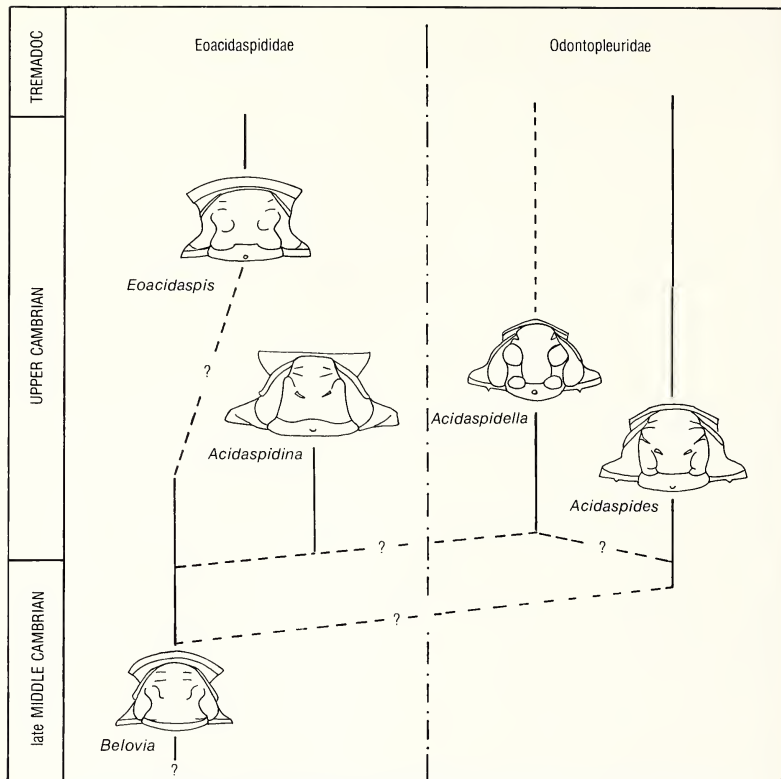
The origin of the Eoacidaspididae is unknown and more skeletal parts (pygidia, free cheeks, details of ventral sutures, etc.) are needed before comparison with earlier stocks is possible. Kobayashi (1962) and Kobayashi and Hamada (1977) have suggested a relationship with the Corynexochida, but studies on the ontogeny of a representative of this group (Robison 1967) show no resemblance to early growth stages among the Eoacidaspididae. Likewise, the relationship between the Eoacidaspididae, the Amgaspidae Tchernysheva, 1960, and Bestjubbellidae Ivshin, 1962, is particularly obscure and type material needs to be examined before further remarks can be made.

Genus EOACIDASPIDIS Poletaeva, 1956

Plate 88, figs. 3, 4, 8, 9

Type species. *Eoacidaspis salairica* Poletaeva, 1956, p. 175, pl. 32, figs. 5, 6, upper Cambrian, Salair Ridge, western Siberia.

Other species. *E. amplicauda* Lazarenko, 1968, p. 196, pl. 18, figs. 10-16.



TEXT-FIG. 2. Morphological grouping of the Cambrian Eoacaspidae and Odontopleuridae.

Diagnosis. Glabella waisted at approximately half sagittal length, dorsal furrows sinuous and deep especially posteriorly. L2 with independent convexity, longest axis oblique at 45° to sagittal line; S1 deepest around base of lobe, very deep on internal mould. L1 flat, weakly developed except posteriorly at lateral deepening of occipital furrow. S2 and S3 short, transverse furrows. Sutures strongly divergent. Surface with granules forming raised pattern.

Discussion. The cranidium (Pl. 88, figs. 8, 9), which is an internal mould, is one of several original paratypes of *E. salairica*, while the cranidium (Pl. 88, figs. 3, 4) is of topotype material of *E. amplicauda* Lazarenko, 1968. Both show the pronounced oval L2 lobe and the more quadrate L1 lobe, especially pronounced on the internal mould. All previously illustrated material, including that by Rozova (1968, pl. 9, fig. 19) is from the western part of Siberia where it occurs in the late upper Cambrian.

Chugaeva and Apollonov (1982, text-fig. 1) list an occurrence as '*Eoacidaspis*' near to the Cambrian-Ordovician boundary in Kazakhstan.

Poletaeva (1957, pp. 162-163) listed *Paraacidaspis* *nom. nud.* and later (1960a, p. 68, pl. 3, fig. 1) diagnosed the genus and figured the holotype of the type species, *P. hunanica* Jegorova in Poletaeva, 1960, *nom. nud.*, from the upper Cambrian Ch'an-shan Stage, Hunan Province, south China. Since the type species was not formally described, the genus *Paraacidaspis* is invalid. Study of the cranidium of *P. hunanica* *nom. nud.* and a second species, *P. sibirica* Poletaeva, 1960 (p. 70, pl. 3, fig. 2) from the upper Cambrian of western Siberia, leaves little doubt that *Paraacidaspis* is a subjective synonym of *Eoacidaspis*.

Stratigraphical and geographical distribution. Late upper Cambrian-basal Ordovician. Salair Ridge, western Siberia, Kazakhstan.

Genus *Belovia* Poletaeva, 1956

Plate 88, figs. 1, 2

Type species. *Belovia calva* Tchernysheva in Poletaeva, 1956, p. 174, pl. 32, fig. 10, from late middle Cambrian, Olenek River, eastern Siberia.

Other species. *B. salairica* Poletaeva, 1960b, p. 241, pl. 27, fig. 17; *B. aliquantula* Rozova, 1964, p. 54, pl. 4, fig. 21; *B. laeta* Rozova, 1964, p. 55, pl. 14, figs. 8-9; *B. cyclica* Rozova, 1964, p. 56, pl. 17, figs. 14-16; *B. media* Poletaeva, 1977, p. 72, pl. 1, fig. 1; *B. radugini* Poletaeva, 1977, p. 70, pl. 1, fig. 2.

Diagnosis. Glabella waisted at approximately half sagittal length and level with S1 furrow. Latter transverse at inner end, moderately deep. L1 and L2 faintly defined. S2 and S3 faint. Anterior portion of glabella weakly defined, tapering forwards, rounded frontal lobe, posterior portion expanding backwards with well-defined dorsal furrows and occipital furrow. Occipital ring narrow and smooth. Fixed cheeks widest opposite S1, rapidly tapering forwards, here eye ridge and lateral parts of glabella in contact. Eyes level with S1. Sutures strongly divergent. Frontal glabellar lobe separated by deep furrow from flattened and raised anterior border. Latter curved. Surface smooth.

Discussion. The holotype by monotypy of the type species (Pl. 88, figs. 1, 2) was described by Tchernysheva (p. 174) in the same publication as that in which Poletaeva (1956, p. 173) established the genus. The type species is from the late middle Cambrian where it is common in beds belonging to the so-called Siligiz Horizon equivalent to the Swedish middle Cambrian Zone of *Lejopyge laevigata*. One species, *B. cyclica* Rozova, 1964 has been recorded from the upper Cambrian Zone of *Agnostus pisiformis*.

Originally *Belovia* was assigned by Poletaeva (1956) to the Odontopleuridae but later (Poletaeva 1957, 1960a) it was placed in the Eoacidaspididae together with the younger *Eoacidaspis* and *Paraacidaspis* *nom. nud.* *Belovia* and *Eoacidaspis* have in common the waisted glabella, sinuous dorsal furrows, the diverging anterior facial surface, and the prominent rim along the anterior border. *Eoacidaspis* has more prominent L1 and L2 lobes and a broader occipital ring.

Numerous described and undescribed species of *Belovia* show a whole plexus of evolving forms with transitional morphotypes from *Belovia* to *Eoacidaspis*.

Stratigraphical and geographical distribution. Late middle Cambrian to early upper Cambrian, northern and north-west Siberian Platform, eastern Siberia, Olenek River and western Siberia, Salair Ridge.

Genus *Acidaspidina* Lazarenko, 1960

Plate 88, fig. 13

Type species. *Acidaspidina plana* Lazarenko, 1960, p. 39, pl. 4, figs. 9-12, from early upper Cambrian, Yenisey River, north-west Siberian Platform.

Diagnosis. Glabella moderately convex, outlined along entire length by straight to gently sinuous dorsal furrows. L2 most prominent adjacent to dorsal furrow, base marked by short, deep slot of S1.

L1 weak. S2 short, backwardly directed, S3 transverse. Fixed cheeks widest posteriorly, tapering forwards, and dying out opposite outer end of S3. Occipital ring broad (sag.), furrow curved forwards. Small occipital tubercle near posterior margin. Anterior and posterior facial sutures strongly divergent. Surface finely granulated.

Discussion. The cranidium (Pl. 88, fig. 13) is that figured by Lazarenko 1960, pl. 4, figs. 9–10, from the early upper Cambrian Zone of *Glyptagnostus stolidus* on the north Siberian Platform. Here the genus occurs together with species of *Belovia* and *Acidaspidella* and is seemingly intermediate between the two in that the dorsal furrow is straighter than it is in *Belovia* and the glabellar furrows are more pronounced though not as much as in *Acidaspidella*. Lazarenko (1960, p. 40) believed *Acidaspidina* to be close to *Acidaspides* but the latter does not have the strongly divergent anterior facial suture and the glabellar lobes are more distinct. Features of the glabellar lobation and the anterior border are more clearly seen in specimens of *A. plana* described and figured by Rozova (1968, p. 88, pl. 3, figs. 16–18) and by Zuravleva and Rozova (1977, p. 68, pl. 3, figs. 7–10).

The type of pygidium associated with *Acidaspidina* by Lazarenko (1960, pl. 4, figs. 11–12) was thought by her to be similar to those assigned to the Anomocaridae. This is probably correct but the cranidium of *Acidaspidina* does not belong to that family.

Stratigraphical and geographical distribution. Early upper Cambrian (Chomurdakh Horizon), north Siberian Platform.

Family ODONTOLEURIDAE Burmeister, 1843 (emend. Whittington, 1956)

Genus *Acidaspides* Lermontova, 1951

Plate 88, figs. 7, 11, 12, 14–18

Type species. *Acidaspides precurrens* Lermontova, 1951, p. 27, pl. 6, figs. 4–9, from upper Cambrian, Kazakhstan.

Other species. *A. lermontovae* Tchernysheva, 1953, p. 81, pl. 6, figs. 16–17; *A. borealis* Tchernysheva, 1960b, p. 254, pl. 53, figs. 9–10.

EXPLANATION OF PLATE 88

All photographs are those of plaster casts except for figures 8, 9 which are of an actual specimen. CGML = Central Geological Museum, Leningrad; PMO = Paleontologisk Museum, Oslo.

Figs. 1, 2. *Belovia calva* Tchernysheva in Poletaeva, 1956. Holotype, CGML 20/8505, PMO 108.537, dorsal and oblique frontal view, $\times 2$. Original of Tchernysheva in Poletaeva 1956, pl. 32, fig. 10.

Figs. 3, 4. *Eoacidaspis amplicauda* Lazarenko, 1968. PMO 108.539, frontal and dorsal view, $\times 2$. Upper Cambrian, north-west Siberian Platform.

Figs. 5, 6, 10, 19. *Acidaspidella* sp. cf. *A. limita* Rozova, 1963. 5, PMO 108.534, dorsal view, $\times 5$. 6, PMO 108.524, dorsal view, $\times 5$. 10, 19, PMO 108.541, oblique lateral view, $\times 3$, and dorsal view, $\times 3$. Upper Cambrian, Kulyumbe River, north-west Siberia. This material is the same as that listed as *A. bella* Pokrovskaya, 1961 *nom. nud.*

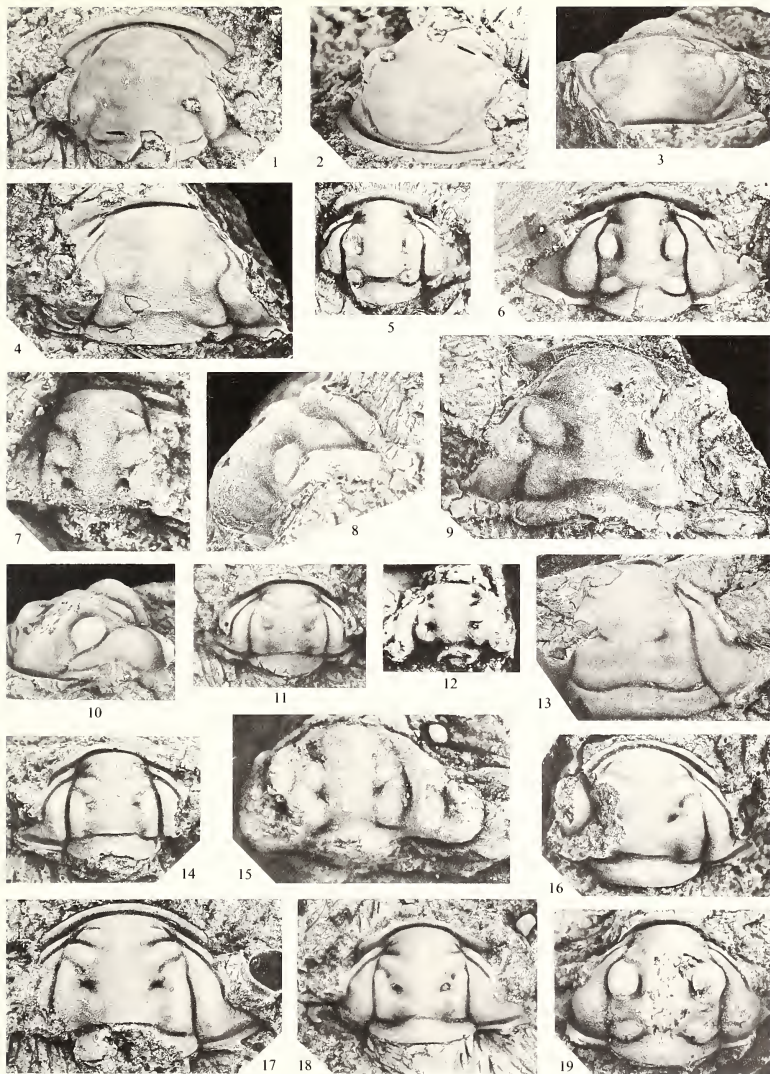
Fig. 7. *Acidaspides lermontovae* Tchernysheva, 1953. CGML 93/7109, PMO 108.533, dorsal view, $\times 9$. Late middle Cambrian, Aldan River, eastern Siberia. Original of Tchernysheva 1953, pl. 6, fig. 17.

Figs. 8, 9. *Eoacidaspis salairica* Poletaeva, 1956. Paratype, PMO 108.538, left lateral and dorsal views, internal mould, $\times 2$. Upper Cambrian, Salair Ridge, western Siberia.

Figs. 11, 14, 16–18. *Acidaspides borealis* Tchernysheva, 1960. 11, CGML 34/9180, PMO 108.535, dorsal view, $\times 6$, original of Tchernysheva 1960, pl. 53, fig. 9. 14, CGML 35/9180, PMO 108.523, dorsal view, $\times 5$, original of Tchernysheva 1960, pl. 53, fig. 10. 16, PMO 108.527, dorsal view, $\times 6$. 17, PMO 108.526, dorsal view, $\times 5$. 18, PMO 108.540, dorsal view, $\times 3$. Upper Cambrian, Olenek River, north-east Siberia.

Figs. 12, 15. *Acidaspides precurrens* Lermontova, 1951. 12, paralectotype, CGML 56/7350, PMO 108.528, dorsal view, $\times 10$, original of Lermontova 1951, pl. 6, fig. 7. 15, lectotype (here chosen), CGML 53/7350, PMO 108.530, dorsal view, $\times 10$, original of Lermontova 1951, pl. 6, fig. 4. Upper Cambrian, Kazakhstan.

Fig. 13. *Acidaspidina plana* Lazarenko, 1960. CGML 45/8617, PMO 108.532, dorsal view, $\times 2$. Original of Lazarenko 1960, pl. 4, figs. 9, 10. Upper Cambrian, Yenise River, north-west Siberia.



BRUTON, Cambrian odontopleurid trilobites

Diagnosis. Holaspid and juvenile crania with L1 the larger lobe, at least twice the size of L2, widest at base, tapering forwards, longest axis parallel to dorsal furrow. S1 directed backwards and inwards at 45°, deepest adjacent to dorsal furrow, separated by raised bridging area from circular pit at inner end. S2 short, backwardly and inwardly directed, S3 transverse. Dorsal furrows gently curved convex outwards, deepest posteriorly. Eye ridges narrow, eyes positioned opposite anterior half of L1. Occipital ring with backwardly curved posterior margin, small occipital spine. Anterior branch of facial suture straight, posterior branch diverging outwards at slightly greater than 90°. Posterior border furrow deep, margin with short spines. Anterior border furrow narrow, deep, margin upturned. Surface with fine granules.

Discussion. The cranium figured by Lermontova (1951, pl. 6, fig. 4) is here selected as lectotype for the type species *A. precurrens*. This is refigured herein as Pl. 88, fig. 15, together with an additional cranium (Pl. 88, fig. 12), figured by Lermontova (1951, pl. 6, fig. 7), which is selected as paralectotype. Both specimens are juvenile stages or very young holaspids and show remarkably many of the characteristic features of certain post-Cambrian odontopleurids. These include the small L3 lateral lobe known in *Primaspis* and *Miraspis*, the palpebral lobe and posterior part of the fixed cheek overhanging the posterior margin as in *Miraspis*, and prominent paired spines on the median glabellar lobe, a feature of the Miraspidinae.

The exact stratigraphical range of the type species is somewhat in doubt. It was originally recorded from the local Kazakhstan Zone of *Lotagnostus trisectus*, thought to be equivalent to the Swedish upper Cambrian Zone of *Peltura scarabaeoides*, although it could be as young as basal Tremadoc. Reasons for this are based on hitherto undescribed material of *A. cf. precurrens* from the so-called Chokuk Horizon of the Anabar Massif.

A pygidium was assigned to *A. precurrens* by Lermontova (1951, pl. 6, fig. 8) on account of its spinose posterior margin. It is the only specimen of this type known and its affinity with the crania is very doubtful, as acknowledged by Lermontova.

A number of well-preserved crania of *A. borealis* Tchernysheva, 1960 are known from the basal upper Cambrian of the Olenek River. These include two of the crania figured by Tchernysheva (1960b, pl. 53, figs. 9, 10; Pl. 88, figs. 11, 14 herein) and three additional crania, all topotypes. This material is of holaspids and is amongst the best preserved of any Cambrian odontopleurids. The resemblance to members of the Miraspidinae is less obvious and the glabellar lobation more closely resembles that of early members of the Odontopleurinae including *Primaspis whitei* Whittard, 1961 and *P. multispinosa* Bruton, 1965 from rocks of Llandeilo age in Norway, Salop, and South Wales (see Bruton 1965, p. 11). In this respect the structure of L1 in *A. borealis* is of interest because it has a posterior furrow partly delimiting a small subsidiary basal lobe. Such a lobe becomes separated in early *Primaspis* to form the occipital lobe (cf. *P. whitei* Whittard, 1961, pl. 27, figs. 3, 4). This feature is also known in species of *Odontopleura* (*O. ovata*; see Bruton 1968, pl. 1, fig. 1). *Acidaspis* (*A. cincinnatiensis*; see Whittington 1956a, pl. 59, fig. 9), and in *Diacanthaspis* it is either well developed or scarcely so (Whittington 1956b, p. 211).

The resemblance of holaspid *Acidaspidetes* and *Acidaspidella* to the *Primaspis*–*Leonaspis* group thus extends the stratigraphical range of the root-stock of the Odontopleurinae (cf. Whittington 1956b, p. 90, 1966). Early growth stages of *Acidaspidetes* also resemble members of the Miraspidinae suggesting that this subfamily is closer to the Odontopleurinae than previously thought.

The earliest occurrence of *Miraspis*, from the Arenig of Sweden (Whittington and Bohlin 1958), shows that the Miraspidinae must have been already well differentiated before this time.

Acidaspidetes lermontovae Tchernysheva, 1953 is based on an early growth stage from the Maya Stage, Aldan River, eastern Siberia, in beds equivalent to the Swedish middle Cambrian Zones of *Lejopyge laevigata* and *Triplagnostus lundgreni*. Whilst not well preserved, the cranium (Pl. 88, fig. 7) does show three glabellar lobes and the characteristic S1 furrow with shallow median bridging portion separating the outer furrow from an inner pit.

Stratigraphical and geographical distribution. Middle Cambrian, Aldan River, eastern Siberia. Upper Cambrian, Olenek River, north-east Siberia, Kazakhstan.

Genus *Acidaspidella* Rozova, 1963

Plate 88, figs. 5, 6, 10, 19

Type species. Acidaspidella limita Rozova, 1963, p. 9, pl. 1, fig. 4, from the early upper Cambrian, Kulyumbe River, north-west Siberian Platform.

Diagnosis. Glabella and fixed cheeks strongly convex. Dorsal furrows curved around outer surface of L2. Latter the larger, most prominent, completely circumscribed by S2. S1 broad and shallow. L1 outlined by independent convexity and deepened outer portion of occipital furrow around base. Longitudinal furrows shallow, median glabellar lobe rectangular with long anterior portion. L3 short, backwardly directed and lying in pit at end of eye ridge and fixed cheek. Occipital ring longest (sag.) with centrally placed tubercle. Anterior border furrow narrow, margin turned dorsally. Eyes positioned on transverse line through L2. Anterior branch of facial suture directed straightforward from base of eye, posterior branch directed outwards at a little more than 90°. Dorsal surface granulated, spine from posterior margin.

Discussion. Rozova (1964, p. 57) attributed the authorship of the genus to Pokrovskaya, but selected *A. limita* Rozova, 1963 as type species. Dr. Pokrovskaya (pers. comm.) informs me that *Acidaspidella* Pokrovskaya 1961 *nom. nud.* was still undescribed in 1963 and that Rozova is to be considered the author of the genus. I have not seen the type material, but that figured herein from the collections of Drs. Lazarenko and Pokrovskaya is probably the same species. All this material is from the Sukan and Kulyumbe River areas on the north and north-west Siberian Platform. It was listed as *A. bella* Pokrovskaya, 1961 *nom. nud.*, p. 268, and occurs in the early upper Cambrian Zone of *Glyptagnostus stolidus*.

As in the younger *Eoacidaspis*, the L2 glabellar lobe of *Acidaspidella* is the most prominent but the longest axis of the lobe is parallel to an exsagittal line and not oblique to it. Two small specimens including the one figured on Pl. 88, fig. 6, show the broken bases of spines along the posterior margin but these cranidia are probably those of holaspids. *Acidaspidella* and *Acidaspides* both have a convergent anterior facial suture and a narrow upturned anterior border. In *Acidaspidella*, however, the independent convexity of the lateral lobes, the deepened longitudinal furrow, and the long frontal lobe with effaced L3 are distinguishing features. *Acidaspidella* is placed in the Odontopleurinae because of its resemblance to *Odontopleura* and *Leonaspis*.

Stratigraphical and geographical distribution. Early upper Cambrian, Yenise River, eastern Siberia. Upper Cambrian-?basal Ordovician (Chokuk Horizon), northern Siberian Platform.

Acknowledgements. Travel to, and within, the Soviet Union in 1965 was arranged and financed through the generosity of the British Council and the Soviet Academy of Sciences. Help received from the staff of these organizations and from Drs. M. N. Chugaeva and N. V. Pokrovskaya (Moscow) and Drs. N. P. Lazarenko and N. E. Tchernysheva (Leningrad) is most gratefully acknowledged. Finally, I record my gratitude to the staff of the Russian Translation Service, National Lending Library, G.B., and to my colleague Natascha Heintz, for providing me with the translations of the literature required for this study.

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THE PALAEOONTOLOGICAL ASSOCIATION

ANNUAL REPORT OF COUNCIL FOR 1982

MEMBERSHIP AND SUBSCRIPTIONS. Membership totalled 1,465 on 31 December 1982, a decrease of 23 over the previous year. There were 942 Ordinary Members, a decrease of 14; 35 retired Members, an increase of 7; 158 Student Members, an increase of 9; and 330 Institutional Members, a decrease of 25. The number of institutions subscribing to *Palaentology* through Marston's agency was 445, an increase of 26. Subscriptions to *Special Papers in Palaentology* number 140 individual, a decrease of 24, and 128 Institutional, a decrease of 10. Subscriptions to *Special Papers* through Marston's agency were 60 for *Special Paper 28*; figures for *Special Paper 29* are not yet available. Sales of back parts of *Palaentology* via the Membership Treasurer totalled 47 transactions realizing £2,426, a spectacular increase reflecting the popularity of the special offer. Sales of back copies of *Special Papers* rose to 88 transactions, realizing £1,462. Sales of back parts of *Palaentology* to Institutional Members yielded £75 plus U.S. \$37. Sales of *Special Papers* to Institutional Members yielded £107 plus U.S. \$71.

FINANCE. During 1982 the Association published Volume 25 of *Palaentology* at an estimated cost of £50,077 (including postage and distribution). *Special Papers 28* and *29* were published at a cost of £12,296. In addition, *Atlas of the Burgess Shale* was published at a cost of £3,171 (exclusive of postage). The Association is grateful to all who made donations.

PUBLICATIONS. Volume 25 of *Palaentology*, published in four parts during 1982, contained 923 pages and 100 plates. *Special Paper 28*: 'The mammal fauna of the early Middle Pleistocene cavern infill site of Westbury-sub-Mendip, Somerset' was published in August 1982 and *Special Paper 29*: 'Fossil cichlid fish of Africa' in October 1982.

MEETINGS. Eight meetings were held in 1982. The Association is indebted to the organizers, hosts, and field leaders.

- a. *Review Seminar* on 'Echinoderm evolution and adaptation' held on 10 February at the University of Liverpool. Twenty-five attended the meeting. The local secretary was Dr. A. B. Smith.
- b. *Silver Jubilee Day and Annual General Meeting*, held at Imperial College, London, on 26 February. Professor S. J. Gould and Dr. C. Patterson delivered the addresses on 'Palaentology, evolution and systematics'. The Sylvester-Bradley Award was made to Mr. P. Ensom and Mr. P. Hodges. The meeting was followed by a dinner.
- c. *Field Meeting*, organized by the Carboniferous Group, to the 'Carboniferous of the Craven Basin' led by Dr. N. J. Riley and others. Seventy attended the excursion which was held on 16-19 April.
- d. *Review Seminar* on 'Palaecobiology of animal colonies' held on 5 May at the British Museum (Natural History), London. Forty-five attended the meeting. The local secretary was Dr. P. D. Taylor.
- e. *Symposium on Vertebrate Palaentology* held on 8-9 September at the British Museum (Natural History), London. This meeting was co-sponsored with the Geological Curator's Group. Sixty attended. The local secretary was R. J. Cleevely.
- f. *A Symposium on Fossils and Climate* was held jointly with the Liverpool Geological Society on 23-24 September as part of the Geological Societies of Great Britain Meeting at the University of Glasgow. The secretaries for the symposium were Dr. P. J. Brenchley and Dr. G. Newall. Fifty attended. The meeting included an Extraordinary General Meeting of the Association.
- g. *Field Meeting* on the 'Upper Jurassic and Cretaceous of Normandy' was held on 1-4 October, and led by Dr. P. Juignet and Dr. M. Rioult. Twenty attended. The organizing secretary was Dr. J. M. Hancock.
- h. *The Annual Conference*, held at the University of Sheffield on 12-15 December, took the form of an open meeting. One hundred and fifty-four attended. The President's Award was made to Dr. T. H. Jefferson. An excursion led by Dr. I. M. Simpson and Dr. G. M. Walkden examined the 'Sedimentology and palaecology of the south-east margin of the Derbyshire carbonate platform'. The local secretary was Dr. M. Romano.

COUNCIL. The following members served on Council following the A.G.M. on 26 February 1982: *President*, Professor A. Hallam; *Vice-Presidents*, Professor J. W. Murray, Dr. R. A. Fortey; *Treasurer*, Dr. M. Romano; *Membership Treasurer*, Dr. J. C. W. Cope; *Secretary*, Dr. R. Riding; *Marketing Manager*, Dr. R. J. Aldridge; *Editors*, Dr. K. C. Allen, Dr. M. G. Bassett, Dr. D. E. G. Briggs, Dr. L. B. Halstead; *Other Members*, Dr. C. H. C. Brunton (Institutional Membership Treasurer), Dr. E. N. K. Clarkson, Dr. D. Edwards, Dr. R. Harland, Dr. P. D. Lane, Dr. A. R. Lord, Dr. J. Miller, Dr. T. J. Palmer, Dr. D. J. Siveter, Dr. P. W. Skelton (Circular Reporter), Dr. P. D. Taylor, Dr. A. Thomas, Dr. H. S. Torrens, Dr. N. H. Trewin.

CIRCULARS. Four Circulars, numbers 107-110, were distributed to Ordinary, Retired, and Student Members, and on request to over 100 Institutional Members during 1982.

COUNCIL ACTIVITIES. During 1982 the Association celebrated its Silver Jubilee with the highly successful afternoon of lectures, followed by dinner, in London on 26 February. The programme of field meetings, symposia, and review seminars continued as normal and was well-supported. In addition to its regular publications the Association also published the *Atlas of the Burgess Shale*. Plans for future meetings include the 'Symposium on autecology of Silurian organisms' and conference on 'Evolutionary case histories from the fossil record', and progress has been made with the preparation of a new series of publications. Council is actively exploring ways to revise its internal structure in order to improve efficiency.

BALANCE SHEET AND ACCOUNTS FOR THE YEAR ENDING 31 DECEMBER 1982

BALANCE SHEET AS AT 31 DECEMBER 1982

1981			
£	£		£
45,843		INVESTMENTS AT COST (see schedule)	46,586
		CURRENT ASSETS	
	2,635	Sundry debtors	3,824
	12,880	Cash at bank	12,705
	<u>15,515</u>		<u>16,529</u>
		CURRENT LIABILITIES	
	881	Subscriptions received in advance	339
	12,000	Provision for publication of <i>Palaeontology</i> Vol. 25, Pt. 4	13,250
	1,959	Sundry creditors	2,026
	<u>14,840</u>		<u>15,615</u>
675		Excess of current assets over current liabilities	914
<u>£46,518</u>			<u>£47,500</u>
Represented by:			
		PUBLICATIONS RESERVE ACCOUNT	
	39,127	Balance brought forward	42,218
	3,091	Excess of income over expenditure for the year	947
42,218	<u> </u>	Balance carried forward	<u>43,165</u>
		SYLVESTER BRADLEY FUND	
		Balance brought forward	2,010
		Interest received	211
		Grants awarded	(200)
		Balance carried forward	<u>2,021</u>
2,010		MEETING RESERVE	2,314
2,290			
<u>£46,518</u>			<u>£47,500</u>

INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR ENDED 31 DECEMBER 1982

INCOME

[illegible]

EXPENDITURE

	COST OF PUBLICATION OF <i>PALAEONTOLOGY</i>		
	Volume 25—Part 1	12,015	
	Part 2	11,772	
	Part 3	13,040	
	Part 4 (provisional)	13,250	
47,985	Under provision for Vol. 24, Pt. 4	607	
	COST OF PUBLICATION OF <i>SPECIAL PAPERS</i>		50,684
	No. 28	6,031	
9,217	No. 29	6,265	
	WAREHOUSING OF PUBLICATIONS		12,296
	COST OF CIRCULARS		2,355
	Preparation	3,652	
	Postage	1,430	
4,663	Credit	(150)	
18	OFFPRINTS—LOSS		4,932
	COST OF BURGESS SHALE PORTFOLIO		916
	Publication costs/postage	3,553	
	Sales	2,313	
	ADMINISTRATIVE EXPENSES		1,240
	Postage and stationery	1,300	
	Editorial expenses	223	
	Meeting expenses	1,479	
	Membership of societies	15	
4,012	Audit fee	200	
			3,217
£65,895			£75,640
	EXCESS OF INCOME OVER EXPENDITURE FOR THE YEAR TRANSFERRED TO PUBLICATIONS RESERVE ACCOUNT		£947

SCHEDULE OF INVESTMENTS AND INVESTMENTS INCOME AS AT 31 DECEMBER 1982

		Cost £	Gross Income for Year £
12,000	13½% Exchequer Stock 1987	11,520	1,590
1,000	9% Treasury Stock 1992/1996	992	90
1,000	9% Treasury Stock 1994	955	90
4,000	8% Treasury Stock 2002/2006	2,192	320
5,357	13½% Treasury Stock 1997	5,000	710
3,280	13½% Exchequer Stock 1996	3,000	435
2,000	Agricultural Mortgage Corporation Ltd. 9¼% Debenture 1980/1985	1,938	185
5,270	M. & G. Charifund units	4,073	964
2,425	Imperial Group p.l.c. 8% Convertible Unsecured Loan Stock 1985/1990	1,730	194
10,000	New Throgmorton Trust p.l.c. 25p Income Shares	1,706	286
1,600	Commercial Union Assurance Co. p.l.c. 25p Shares	2,157	270
700	Clarke, Nicholls & Coombs p.l.c. 25p Shares	668	27
5,000	Thorn EMI p.l.c. 7% Convertible Redeemable Second Cumulative Preference £1 Shares 1992/1999	5,009	500
6,180	M.E.P.C. p.l.c. 6½% Convertible Unsecured Loan Stock 1995/2000	4,943	402
374	M.E.P.C. p.l.c. 25p Shares	703	28
	Bank Interest		6,091
		46,586	1,805
	MARKET VALUE at 31 December 1982 (1981—£48,977)	£57,589	

REPORT OF THE AUDITOR TO THE MEMBERS OF
THE PALAEONTOLOGICAL ASSOCIATION

In my opinion, the Accounts as set out on pages 889–891, give a true and fair view of the state of the affairs of the Association at 31 December 1982, and of its income and expenditure for the year ended on that date.

February 1983

Market Harborough, Leicestershire

G. R. POWELL
Chartered Accountant

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